

## A single comma in a manuscript alters Mauritius avian history

Anthony S. Cheke  
139 Hurst St., Oxford OX4 1HE, UK  
[anthony.cheke@dodobooks.com](mailto:anthony.cheke@dodobooks.com)

Strickland's famous book (1848) on the extinct Dodo *Raphus cucullatus* contains a number of transcribed accounts from early Dutch visitors to Mauritius, including the following passage from an account by Reyer Cornelisz (Commelin 1646) reporting a visit from April to September 1602:

*In this country occur tortoises, wallichvogels [Dodos], flamingos, geese, ducks, field-hens, large and small Indian ravens, doves, some of which have red tails (by eating which many of the crew were made sick), grey and green parrots with long tails, some of which were caught* [Strickland's translation, except that I have replaced 'crows' with 'ravens' to reflect the original Dutch]

From this it has always been assumed that Cornelisz had seen two sizes of 'Indian Raven', interpreted, when noticed at all, as sexual dimorphism (Hume 2007, Cheke & Hume 2008). In the Mauritian context the term 'Indian Raven' has long been known to refer to the large extinct parrot *Lophospittacus mauritianus* (e.g. Newton & Newton 1876). Holyoak (1973) described a second species as *L.bensoni*, not the smaller 'raven', but the grey parrot of Cornelisz's text, now known to be a *Psittacula*, and named Thirioux's Grey Parrot (Hume 2007). *L.mauritianus*, the Raven Parrot, was strongly sexually dimorphic (Holyoak 1971, Hume 2007), so once that was established, the original text made sense.

More recently however, Parmentier *et al.* (2003) have published a full transcript of the original manuscript containing Cornelisz's account, and it shows that Commelin had edited the bird list, transferring the position of a comma that radically alters the sense of the sentence. The new version reads:

*[here is something] about the animals found there in that land, such as tortoises, walchvogels [Dodos], flamingos, geese, ducks, [birds] like field-hens large and small, Indian ravens, also doves, there are also red-tailed doves, there [=through (eating) which] many men have been ill, here are also many grey parrots, finally also green [ones] with long tails, some of which were captured* [my translation, with help from Sewel (1766), as many words in the Dutch text are no longer in modern dictionaries]

Thus the adjectives ‘large’ and ‘small’ are shown to clearly refer to the ‘hens’ (*veldthoenders*) not the parrots (*raves*). *Veldthoen* (and cognates), then used back in Holland for partridges, was the standard term used by 17th century Dutch visitors and colonists for the Red Hen *Aphanapteryx bonasia* (Cheke & Hume 2008). We know from subfossil bones (Cheke & Hume 2008, Hume & Walters 2012) that there were two species of flightless rails, the large chicken-sized Red Hen and a smaller species in the genus *Dryolimnas*, the size of a Moorhen *Gallinula chloropus* and not yet formally described: Sauzier’s Wood Rail (*ibid.*). Up until now we had no account that clearly referred to the smaller rail, but the revised account from Cornelisz shows that he recognised the two species, and that Sauzier’s Wood Rail was thus still extant when the Dutch first visited the island. There are no further reports, and it presumably succumbed to rat or pig predation on its nests in the years that followed.

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## Appendix: original Dutch text of the above quotations

1. Commelin (1646: 30): *Op het lant onthouden haer Schilt-padden/ Wallichvogels/ Flamencos/ Gansen/ Eendt-vogels/ Velt-hoenders/ so groot as kleyne Indiaensche Ravens/ Duyven/ daer onder sommige met roo steerten/ (van de welcke menig man sieck geweest is), grauwe ende groene Papegayen, mey lange steerten/ waer van datter sommige ghevangen werden.* [transcribed from the original black-letter text; note the position of the slashes (/), used by Commelin instead of commas, clearly linking the ‘so groot als kleyne’ to the Indian Ravens]

2. Parmentier *et al.* (2003:164): *Item vande gedierten dy er haer opt landt onthouden, als schiltpadden, walchvogels, flamenchus, ganssen, entvoegelen zoo velthoenderen groot en kleyn, Indiaenschen ravers, oyck duyven, daer syn oyck roostarte duyven, daer menich man sieck aff geweest is, hier syn oyck menichete van grauwe papegaeyen, ende oyck groene met lanhe starten, waervander sommige gevanghen worden...* [there should, I believe, be a comma after ‘entvoegelen’]

## **Extinct birds of the Mascarenes and Seychelles - a review of the causes of extinction in the light of an important new publication on extinct birds**

Anthony S. Cheke  
139 Hurst St., Oxford OX4 1HE, UK  
[anthony.cheke@dodobooks.com](mailto:anthony.cheke@dodobooks.com)

*Extinct birds* by Hume & Walters (2012) is the most comprehensive treatment of extinct avian species ever attempted, and the authors are to be congratulated on putting all this material in one place. However in relation to the well-documented Mascarenes there are numerous anomalies and discrepancies, and for the Seychelles some lesser but not unimportant omissions and errors. Only globally extinct species and subspecies are treated in the book, so lost local populations of taxa still extant elsewhere are not included. Since Hume & Walters (hereafter H&W) is so comprehensive, it will undoubtedly be data-mined for causes of extinction. It is therefore important that this record is not confused by erroneous interpretation.

It should be noted that H&W evidently went to press before Hume's treatise on Mascarene pigeons (2011) was published, so some species left undescribed in the book now have valid names.

### **Mascarenes**

Although the putative, or in a few cases known, causes of extinction were explored in my ecological histories (Cheke 1987, Cheke & Hume 2008 [main text by ASC, hereafter C&H]), H&W published for many birds quite different suggested reasons, giving no supporting evidence or even sometimes, erroneously, citing C&H as source. Since the extinction history in the Mascarenes is so well documented, these islands provide a particularly forensic record of generally well-dated extinctions, which can be correlated with humans activities, introduction of alien species etc.

For Rodrigues in particular H&W have adduced a completely undocumented reason for several extinctions that took place between 1725 and 1761: "tortoise hunters who burned off the forest to collect giant tortoises" (*Cylindraspis* spp.) and/or the deforestation that is alleged to have accompanied this practice. In fact the handful of men living there for the sole purpose of collecting tortoises had no reason to clear forest, and there is no evidence they did so. Furthermore, the first documented case of a deliberate bush-fire was in 1761, when the birds in question were already extinct, and was apparently a one-off. Indiscriminate fire-raising (by disaffected slaves) did become a serious problem, but decades later, from 1795 onwards, once agricultural settlement started. While it probably contributed to the extinction of the tortoises, it was too late to have affected the birds. In any case hunting tortoises with fire would have been completely self-defeating, as they were needed alive to transport to Mauritius, and fire



would have simply killed them.

In many cases the extinction date can be correlated with particular invasive species arrivals (C&H). Many ground nesting birds, for instance, survived the arrival of rats *Rattus rattus* and pigs *Sus scrofa*, but rapidly succumbed when cats *Felis 'catus'* arrived. On both Mauritius and Réunion the first actual report of cats was after the birds declined or vanished, but in Réunion the cats were discussed precisely because they were blamed for extinctions. In Mauritius the first cat report was independent of extinction observations, but the fact that several ground-nesting birds disappeared shortly before the report is very strongly indicative. At the time the human population was barely in three figures, and the island had plenty of impenetrable forest and many wetlands/swamps, so overhunting is unlikely to have been a major factor for birds, though in Réunion the limited wetlands and larger human population would have made hunting a more important factor for waterbirds. Despite this more specific evidence, in most cases H&W simply vaguely mention 'introduced predators', or wrongly stress rats. Some predators such as Tenrecs *Tenrec ecaudatus*, House Shrews *Suncus murinus* and the Wolf Snake *Lycodon aulicus* will not have affected birds, and the arrival in Mauritius of the Small Indian Mongoose *Herpestes auropunctatus* in 1900 was too late to influence native species, but had a devastating effect on introduced gamebirds. Likewise the Wattle-necked Softshell Turtle *Palea steindachneri* was a late arrival in Mauritius (c.1920), but would no doubt have attacked the young of native waterbirds had they not already been long extinct.

The timing of forest destruction is also important, as blaming 'forest destruction' when only 5-10% of the lowland forest had in fact gone does not hold water. Although agricultural clearances started early, human populations were initially quite low, such that sufficient forest clearance to seriously affect bird populations only occurred in the late 18th century in Réunion and the early 19th on Mauritius. Apart possibly for the very dry west coast of Réunion which was already much altered by c.1725, 18th century and earlier extinctions will almost always have been due to other factors.

To help understand the timings of extinctions related to introduced predators, Table 1 gives dates when the various animals that attack birds were introduced on the three islands; only those animals which arrived when vulnerable native species still existed are included. Pigs, cats and rats all attack ground nesters and reptile eggs, while arboreal birds are targeted by monkeys and Ship Rats.

**Table 1.** Introduction dates of major bird predators in the Mascarenes

Predator	Mauritius	Réunion	Rodrigues
Crab-eating Macaque <i>Macaca fascicularis</i>	1602	-	-
Pig <i>Sus scrofa</i>	1606	1629	c.1792
Cat <i>Felis 'catus'</i>	ca.1685	ca.1685	c.1745
Ship Rat <i>Rattus rattus</i>	pre-1598	1672-3	pre-1691
Norway Rat <i>R.norvegicus</i>	1735	1735	uncertain, pre-1874

The appendix table lists extinct Mascarene birds in the same sequence as in H&W, with the documented or inferred reasons for extinction compared to their version. Locally (but not globally) extinct birds are included for completeness (indicated by ‘\*’), apart from two ‘data deficient’ seabirds in Rodrigues (Crested Tern *Sterna bergii* & Roseate Tern *S.dougallii*) one of which, and possibly both, made it into the 20th century.

In addition there are a few species included in H&W as known only from subfossils, without adequate observations in life, and hence it is unclear if they survived into human historical times:

- ‘Réunion Pochard’ *Aythya* sp., no reliable report alive, insufficient material (one bone) to establish identity, unclear if resident or vagrant, reason for extinction (if such it is) not known
- Mascarene Reed Cormorant *Phalacrocorax (africanus) nanus*, Mauritius: not recorded alive, reason for extinction not known (in the appendix for Réunion).
- Sauzier's Wood Rail *Dryolimnas* sp. [undescribed] is mentioned in passing (H&W:98). The first clear report of this bird in life has been discovered since H&W was published (Cheke 2013); the subfossil bones await description (C&H, H&W). Only reported once, in 1602, the species probably succumbed rapidly to rats &/or pigs.

A specific clarification is required in relation to the assignment of extinct pigeons from Rodrigues. On the basis of the very minimal material then available, Mourer *et al.* (1999) echoed Milne-Edwards (1874) in considering a subfossil sternum to differ generically from a tarsometatarsus, the former (‘*Columba rodericana*’) said by Mourer to resemble *Gallicolumba*, the latter assigned by both to *Streptopelia* (now *Nesoenas*) *picturata*. C&H followed Mourer’s *et al.*’s diagnosis of two species, though Hume (2011) implied that this was dubious as “no characteristic skeletal elements, e.g. cranium or sternum, have yet to be found to substantiate” the occurrence of *picturata* there. He failed to explain that the reason to doubt its former occurrence was that he (Hume) had just re-assigned the element on which the assessment was based to the other, ex-‘*Gallicolumba*’-type, species, *Columba* (now *Nesoenas*) *rodericana*! In the same paper he restored the number of Rodrigues pigeons to two by creating a new species *Alectroenas payendeei* based on previously undescribed material. Further confusion reigns because many previous authors had, somewhat arbitrarily, assigned some or all of the previously known- elements (i.e. *Nesoenas rodericana*) to the genus *Alectroenas* (discussion in Mourer *et al.* 1999 and Hume 2011) - the new *Alectroenas* is thus a quite different entity from the old ‘*Alectroenas*’.

## Seychelles

The causation data for the three species extinctions in the Seychelles they include is largely accurate, but in two cases H&W missed the last occurrences, thus giving too early a bracketing date on the timing of extinction. They also entirely omitted

an important, well-attested, if not specifically identified extinction.

H&W missed some important data for the extinct Chestnut-Flanked white-eye *Zosterops semiflava*, and still treated it as a race of, or close to, the Mayotte species *Z. mayottensis*. This long-held view based on plumage similarity has been superseded by Warren *et al.*'s DNA phylogeny (2006) which showed they were unrelated and part of two quite different invasions of the western Indian Ocean. *Z. semiflava* was part of an early wave with Mascarene white-eyes and *Z. morouniensis* (upland Grande Comore) from Asia, while *mayottensis* derives from a later colonisation from Africa, together with the other Seychelles species *Z. modesta* and birds on Madagascar and lowland Comoros. H&W missed collections of the white-eye on Marianne in 1877 and 1892 (Lantz, Abbott), and Percival Wright's on Praslin (Oustalet 1878, Skerrett *et al.* 2001), and the contemporary attestation of occurrence also on La Digue and possibly Silhouette. The birds thus survived longer than H&W report, and succumbed to rats (absent on Marianne in 1867, Newton 1867) and deforestation around 1900, not 'between 1870 and 1900'; Gerlach (2007) noted that they were gone by 1908. 'Competition with introduced birds', H&W's third reason for extinction, is unsupported and unlikely.

The Seychelles Parakeet *Psittacula wardi* is quoted as having vanished 'between 1881 and 1906' through deforestation and persecution as a crop-pest, but although they cite a captive pair in 1883, they missed a specimen shot on Mahé in 1893 (Skerrett *et al.* 2001). The third full species extinction in Seychelles was the Aldabra Warbler *Nesillas aldabrana* last seen in 1983, probably due, as H&W say, to rats, although, as Gerlach (2007) pointed out, with such a limited range (a few hectares only) the extinction could be due to stochastic effects.

Perhaps the most enigmatic Seychelles extinction is omitted entirely by H&W, namely the 'poule bleu' of the early accounts of the granitic islands, discussed by Lionnet (1984a). This large blue waterhen was clearly, like the 'oiseau bleu' of Réunion, a *Porphyrio*, but as no specimens were collected and no bones have been found, its specific identity remains unclear; the same is true of the Réunion bird that H&W do however include, perhaps because it acquired a scientific name (see appendix). It was hunted, but it disappeared too rapidly after the islands were settled (1770) for that to have been the main cause, which was probably the introduction of Ship Rats by 1773, and cats by 1787 (Cheke 2010) - the bird was last reported in 1775.

The early accounts from the granitic Seychelles (e.g. Lionnet 1984b) also refer to a 'poule pintade', i.e., in contemporary island French usage, a spotted rail, possibly a *Gallirallus*, and a red-plumaged Fody long before *Foudia madagascariensis* was introduced - this may well (Cheke & Rocamora in prep.) have been a second endemic *Foudia*. Neither were reported again after the islands were settled and colonised by rats and cats.

A most significant local extinction in the Seychelles is Abbott's Booby *Papasula abbotti* from the island where it was discovered, Assumption; H&W mention the extinction but not its date. The birds were still present in 1908, but a settlement to extract guano was founded the same year, rapidly destroying the tree cover and hunting out the seabirds, which were gone by 1916, possibly as early as 1909 (Skerrett *et al.* 2001). See appendix for the loss of this species in the Mascarenes.

As H&W discuss extinct subspecies, they include the dilution and near-extinction, through hybridization, of the Seychelles race of the Malagasy Turtle Dove *Nesoenas picturata rostrata*, and the loss of the Amirante race *N.p.aldabrana*, but only in passing the disappearance of the populations on Astove and Assumption through hunting and habitat destruction<sup>1</sup>. The loss of the Assumption race of the White-throated Rail *Dryolimnas cuvieri abbotti* to rats and habitat loss is likewise covered, but not the elimination through habitat loss and over-hunting of populations of Comoro Blue Pigeon *Alectroenas sganzini* on Astove and Providence, Madagascar Coucal *Centropus madagascariensis* on Assumption and Cosmoledo or the Madagascar Bulbul *Hypsipetes madagascariensis* on Astove (Lionnet 1984a, Skerrett *et al.* 2001) - all three survive on Aldabra, as does its race *D.c.aldabranus* of the rail. A natural population of Barn Owls *Tyto alba* on Aldabra vanished mysteriously, last recorded in 1906 (Skerrett *et al.* 2001). Pink-backed Pelicans *Pelecanus rufescens* on St.Joseph were last reported in 1905 when the coconut plantations were still young and the workers still enchanted by the birds' antics, as described later by Dupont (1941, Lionnet 1984c), who writing in 1937, still thought they survived... Lionnet (1984c) and Skerrett *et al.* (2001) attributed their disappearance to human hunting or persecution.

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### Appendix. Supposed causes of Mascarene extinctions compared.

Abbreviations: C&H = Cheke & Hume (2008), H&W = Hume & Walters (2012). Preferred English names are given in bold; where two are shown, the first is from H&W followed by the usage in C&H, preferred by this author. Codes for Flight/Nest site: Flight ability: N = normal, WF = weak, F = flightless. Nest site: A = open nest in shrub/tree, C = cavity above ground (tree or cliff), G = open nest on ground, B = burrow or ground cavity p = presumed (i.e. inferred from relatives elsewhere)

Species	Flight/ Nest site	Extinction date (from C&H)	Cause given in Hume & Walters (2012) [+ ASC comments]	Cause inferred by Cheke & Hume (2008) or (#) this paper
<b>Mauritius Sheldgoose</b> <i>Alopochen mauritiana</i>	N/pG	c.1695 [<1698]	“overhunting & perhaps predation of eggs by introduced predators”	Primarily cats, hunting secondary; survived rats & pigs
<b>Réunion Sheldgoose</b> <i>A.kervazoi</i>	N/pG	c.1700 [<1705]	“overhunting appears to be the primary cause”	Cats + over-hunting; survived rats & pigs
<b>Mascarene Teal</b> <i>Anas theodori</i> : Mauritius	N/pC	c.1700	“overhunting appears to be the primary cause”	Primarily cats, hunting secondary; survived rats & pigs
<b>Mascarene Teal</b> <i>Anas theodori</i> : Réunion	N/pC	c.1700 [<1705]	“overhunting appears to be the primary cause”	Cats + over-hunting; survived rats & pigs
<b>*Réunion Black Petrel</b> <i>Pseudobulweria atterima</i> & <b>Bourne’s Petrel</b> <i>Pterodroma</i> sp. <sup>2</sup> : Rodrigues	N/B	1726-1761	[not included]	not specified; #survived rats, disappeared like so many other species, coincident with the arrival of cats
<b>*Greater Flamingo</b> <sup>3</sup> <i>Phoenicopterus roseus</i> : Mauritius	N/G	c.1770	[not included]	not specified; last reported ca. 1768 when only 3 remained - #almost certainly hunted out

<sup>2</sup> These are combined as the only report was Tafforet’s *fouquets de montagne* (Cheke 1987, C&H:48-9) - he did not describe the birds, which were evidently inland-nesting petrels. Bourne’s Petrel remains *incertae sedis* due to Graham Cowles never having either described or released the subfossil specimens.

*P.atterima* survives, critically endangered, in Réunion (C&H).

<sup>3</sup> Flamingos on both islands apparently bred in small numbers but were supplemented by migrants from Madagascar; Feuilley in 1705 reported up to several thousand at times (Barré *et al.* 1996).

	site	Extinction	Cause in Hume & Walters	Cause inferred
<b>*Greater Flamingo</b> <i>Phoenicopterus roseus</i> : Réunion	N/G	c.1710	[not included]	as Boucher noted in 1710 - hunted out from the very limited available habitat
Réunion Ibis = <b>Réunion Solitaire</b> <i>Threskiornis solitaria</i>	?WF/?G	c.1715	“overhunting & the introduction of predators such as rats & cats are probable reasons for extinction”	Cats; no evidence it was much hunted in the heights once coastal birds had been eliminated; survived rats & pigs
<b>Mauritius Night-heron</b> <i>Nycticorax mauritianus</i>	N/?A	c.1700	“Reasons for extinction are unknown but no doubt introduced predators such as cats & rats were primarily responsible”	Cats & possibly hunting; survived rats, pigs & monkeys
<b>Rodrigues Night-heron</b> <i>N.megacephala</i>	?WF/?A	c.1750	“severe deforestation & introduced predators”	Cats; survived rats; there was no deforestation at this time
<b>Réunion Night-heron</b> <i>N.duboisii</i>	N/?A	c.1700 [could be a bit later]	“the reason for its extinction is unknown, but it would have been subject to the same introduced predators as its relatives on Mauritius & Rodrigues”	Cats & probably hunting pressure
<b>*Dimorphic Egret</b> <i>Egretta dimorpha</i> : Mauritius	N/A	c.1725	[not included]	Probably persecution on only known colony (Ile aux Aigrettes)
<b>*Dimorphic Egret</b> <i>Egretta dimorpha</i> : Réunion	N/A	c.1870	[not included]	#Given long survival, cause of extinction obscure, likely to be hunting-related; could have been exterminated & recolonised



	site	Extinction	Cause in Hume & Walters	Cause inferred
<b>*Frigate-birds</b> <i>Fregata ariel</i> & ? <i>F.minor</i> : Mauritius	N/A	c.1640	[not included]	direct hunting - the Dutch ate them; the sole nest-site was on the mainland near Dutch base settled in 1638; monkeys may have helped.
<b>*Frigate-birds</b> <i>Fregata ariel</i> & ? <i>F.minor</i> : Rodrigues	N/A	?1860s	[not included]	not specified; #breeding ceased while there were still plenty of boobies <i>Sula sula</i> to kleptoparasitize.
<b>*Abbott's Booby</b> <i>Papasula abbotti</i> : Mauritius	N/A	c.1670	“probably hunted to extinction”	Nested up trees on mainland; probably succumbed to monkeys, old birds persisting after rearing young became impossible
<b>*Abbott's Booby</b> <i>Papasula abbotti</i> : Rodrigues	N/A	c.1835	“probably hunted to extinction”	not specified; #said by Pingré (1763) to be the only seabird worth eating and also the rarest, so probably hunted; last known birds caught for science in 1832 (C&H)
<b>*Red-footed Booby</b> <i>Sula sula</i> : Rodrigues	N/A	c.1880	[not included]	Survived locals, but adults slaughtered & chicks decimated for down by British sailors in the 19thC! Last reported 1874.
<b>(Mascarene)</b> <b>Reed Cormorant</b> <i>Phalacrocorax</i> ( <i>africanus</i> ) <i>nanus</i> : Réunion [see text re Mauritius]	N/?G	c.1710	[not specified, but quote included stating that it was not eaten except when very young]	Not a prime hunting target, but wetlands few & easily hunted out; survived rats & pigs, timing suggests cats.



site	Extinction	Cause in Hume & Walters	Cause inferred
Réunion Rail = <b>Réunion Wood Rail</b> <i>Dryolimnas augusti</i>	1675-1705 ?F/G	“it disappeared due to overhunting & predation by introduced mammals, particularly rats & cats”	Hunting pressure would have been minimal, and <i>D.cuvieri</i> on Aldabra copes with rats; it survived rats & pigs for decades, so cats are the most likely culprit.
Mauritius Red Rail = <b>Red Hen</b> <i>Aphanapteryx bonasia</i>	c.1695 F/G	“appeared to be able to survive the onslaughts of human occupation & associated animals including monkey, pigs & rats ... but the introduction of cats proved disastrous”	[as left]
Rodrigues Rail = <b>Leguat’s Rail</b> <i>Erythromachus leguati</i>	c.1750 F/G	“rapid disappearance between 1726 & 1761 suggests that introduced cats were the main culprits, but severe deforestation by tortoise hunters from 1735 who burned off the forest to collect giant tortoises ... may also have contributed significantly”	Cats, helped by direct hunting; survived rats; there was no deforestation at this time
Réunion Blue Gallinule = <b>Oiseau Bleu</b> <i>Porphyrio ‘caerulescens’</i> <sup>4</sup>	c.1720 [not “the end of the 17th century”] WF/G	“primarily due to over-hunting, but the accidental introduction of rats in 1676 would also have made the eggs & chicks extremely vulnerable”	Was hunted, but remote habitat makes this unlikely as final cause of extinction; survived rats & pigs, so timing suggests cats the most likely cause

<sup>4</sup> No subfossils have been found of this bird, so its specific identity remains unclear, and *P.(porphyrio) madagascariensis* is not ruled out; there was an equivalent, and equally unidentified, form in the Seychelles (Lionnet 1984a; see text).

	site	Extinction	Cause in Hume & Walters	Cause inferred
<b>Mascarene Coot</b> <i>Fulica newtoni</i> : Mauritius	N/G	c.1700	“both populations were presumably exterminated through over-hunting & introduced predators”	Not a prime hunting target; survived rats & pigs, timing suggests cats.
<b>Mascarene Coot</b> <i>Fulica newtoni</i> : Réunion	N/G	c.1700 [<1705]	“both populations were presumably exterminated through over-hunting & introduced predators”	Not a prime hunting target, but wetlands few & easily hunted out; survived rats & pigs, timing suggests cats.
<b>Dodo</b> <i>Raphus cucullatus</i>	F/G	c.1640s on mainland, 1662 on offshore islet; some claim 1680s [disputed]	“direct hunting ... was almost certainly not the primary cause. The introduction of Black Rats <i>Rattus rattus</i> , pigs, goats & perhaps monkeys, all [of] which would have been direct threats to eggs & chicks ... are the likely culprits»	Survivors on Ile d' Ambre killed by sailors in 1662; mainland birds survived rats, but pigs, abundant by the 1620s & reported to raid tortoise eggs, are probable main cause, aided by hunting.
<b>Rodrigues Solitaire</b> <i>Pezophaps solitarius</i> <sup>5</sup>	F/G	c.1760(-65?) [not soon after 1733]	[unclear and selective account, but tortoise hunters burning vegetation appear to be blamed; 1755 account missed]	Cats blamed by locals, but Cossigny (1732-55) in 1755 added hunting, as bird was good to eat - probably cats prevented survivors breeding.
<b>Mauritius Wood Pigeon</b> <i>Columba thirionxi</i> [see Hume 2011]	N/?A?C	[unknown]	“over-hunting, predation from Black Rats <i>Rattus rattus</i> & severe deforestation» [in fact no unequivocal evidence it was ever seen by humans, but early accounts do not fully describe all pigeons]	[not included; subfossils not described at the time of publication]

<sup>5</sup> This is the species long thought to have been a sort of dodo - see e.g. C&H:30-31, H&W:377-8

	site	Extinction	Cause in Hume & Walters	Cause inferred
<b>Réunion Pink Pigeon</b> <i>Nesoenas duboisi</i>	N/pA	c.1700 [<1703]	“The arrival of the Black Rat ... appears to have been a major factor (C&H)” [misquote!]	Cats were clearly blamed by authors in 1703 & 1705 for the very recent demise of <i>ramiers</i> (? this species) & slaty pigeons (below); they survived rats for at least 25 years.
<b>Rodrigues Turtle Dove</b> <i>N. rodericana</i> <sup>6</sup> [see Hume 2011]	N/pA	1726-1761	“Leguat ... noted presence of rats ... and it seems they exterminated the ... dove”	Rats confined the birds to breeding on offshore islets before 1691; either rats reached the islets(#), or the very tame birds were killed by cats c.1750.
<b>Mauritius Turtle Dove</b> <i>N. cicur</i> <sup>7</sup> [see Hume 2011]	N/pA	[unknown]	“disappeared by around 1730 as a result of over-hunting, predation from introduced mammals & severe deforestation” [in fact, no unequivocal report of it alive, possibly due to conflation with other pigeons]	[as then considered conspecific with Malagasy Turtle Dove <i>N. picturata</i> , still present, extinction cause not discussed; though extinction & re-introduction accepted as plausible]
<b>Mauritius Blue Pigeon = Pigeon Hollandais</b> <i>Alectroenas nitidissima</i>	N/pA	c.1835 [‘1837’ misquoted from C&H]	“survived humans & introduced predators for over two centuries, so it was almost certainly deforestation that caused its extinction”	Notoriously good to eat and easy to kill, this pigeon would have become very vulnerable to hunting once habitat was severely reduced, as deforestation accelerated from 1810 onwards
<sup>6</sup> Inadequate material previously available had been referred by Mourer <i>et al.</i> (1999) in part to an undescribed genus near <i>Gallicolumba</i> , and in part to <i>Nesoenas picturata</i> , and thus thought to involve two species; echoed by C&H (see text).				

	site	Extinction	Cause in Hume & Walters	Cause inferred
<b>Réunion Blue Pigeon</b> <i>Allectroenas</i> sp. [no subfossils yet found]	N/pA	<1703	“probably disappeared by around 1700 due to over-hunting & predation by introduced rats”	Definitely did not survive cats (see <i>N.duboisii</i> above), but Dubois’s ‘slaty pigeon’ may have been <i>N.picturata</i> [see C&H & Hume 2011:15 <sup>8</sup> ], so the only firm report was in 1619 - extinction ascribed to cats in C&H
<b>Rodrigues Blue Pigeon</b> <i>Allectroenas payandeei</i> [see Hume 2011] <sup>9</sup>	N/pA	[unknown]	? extinct before 1691, probably due to rats [in fact no evidence this species was ever seen by humans]	[not described when C&H published]
<b>Thirionx’s Grey Parrot</b> <i>Psittacula bensoni</i> : Mauritius	N/pC	1760s	“slash & burn forest clearance ... no doubt had a serious effect on tree-cavity nesting species”	not specified; #this bird was prized for the table, and lowland forest clearance would have reduced nesting possibilities & increased threat from hunting.
<b>Thirionx’s Grey Parrot</b> <i>P.benisoni</i> : Réunion	N/pC	?1730s	“regularly hunted for food, but also appears to have been persecuted for damage to crops”	not specified; #as above.
Rodrigues Ring-necked Parakeet = <b>Rodrigues Parakeet</b> <i>P.exsul</i>	N/pC	1876	“a devastating series of cyclones ... perhaps wiped out the last few survivors (Cheke 1987)”	as left, #but prior rarefaction probably due to deforestation and loss of holes to breed in.

<sup>7</sup> Formerly thought to be a local population of *N.picturata*, e.g. Mourer et al. (1999), C&H.

<sup>8</sup> Subfossil small *Nesoenas* bones on Réunion were referred to *Nesoenas picturata* by Mourer et al. (1999), echoed more tentatively by Hume (2011), but it is unclear whether the birds survived throughout, or died out and were re-introduced. Dubois’s mention of ramiers and tourterelles “like those in Europe” is too vague to be useful, and may have simply been another informant’s account of the two pigeons he had just described (slaty and reddish, treated as *Allectroenas* sp. & the larger *Nesoenas duboisii*); the same problem applies to his parrot account.

<sup>9</sup> H&W correctly say “it was not mentioned by Leguat in 1691-3 or Tafforet in 1725-6” - so the bird may already have been extinct. Alternatively the visitors may possibly have conflated the two pigeon species; they gave no clear descriptions, though the ones most familiar to Leguat (Hume 2007:20) were granivorous, hence *Nesoenas* not *Allectroenas*.

	site	Extinction	Cause in Hume & Walters	Cause inferred
Réunion Ring-necked Parakeet = <b>*Echo Parakeet</b> <i>Psittacula eques</i> [as island endemic species in H&W] <sup>10</sup>	N/C	?1750s [<1760]	[not specified]	not specified; #as <i>P.bensoni</i> , but the Paris specimen collected c.1750.
Mascarene Parrot = <b>Mascarin</b> <i>Mascarinus mascarinus</i> : Réunion	N/pC	?1780s [living birds in Paris in 1784]	[not specified]	not specified, and bird not hunted for food, so, as it survived rats & cats #perhaps lowland forest loss deprived it of nest-sites
<b>Rodrigues Parrot</b> <i>Necropsittacus rodericanus</i>	N/pC	?1770s [v.rare in 1761]	“presumably disappeared due to forest clearance, over-hunting & probable rat predation of eggs & chicks”	Confined, as were pigeons, to nesting on lagoon islets by rats before 1691, either rats reached the islets(#), or the birds were gradually killed off by cats.
Réunion Parrot = <b>Dubois’s Parrot</b> <i>?Psittacula borbonicus</i> [in H&W as <i>?Necropsittacus borbonicus</i> ] <sup>11</sup>	N/pC	?1670s	[not specified]	not specified, #but not reported again after rats arrived, so may have been vulnerable like <i>N.rodericanus</i> .

<sup>10</sup> Best considered conspecific with the extant form on Mauritius; no surviving specimen, but good 18thC illustrations, all probably from the same specimen first described by Brisson (1760). H&W’s mention of three specimens was based on my speculative statement (Cheke 1987, Hume 2007) that three specimens reached Paris for three different illustrations; in hindsight this was a dubious assumption - in fact they were probably all the same one (C&H:316, note 226). The idea in H&W that the Edinburgh specimen might have been the one used for the *Planches Enluminées* (attributed by Hume 2007 wrongly to Jones 1987) is nonsense - the bird was collected between 1801 and 1810 by Mathieu, almost certainly in Mauritius (Jones 1987, C&H).

<sup>11</sup> This bird is known from only one description, and lacks subfossils - some authors (see H&W) have suggested it may have been a feral population of some escaped imported pet parrot.

	site	Extinction	Cause in Hume & Walters	Cause inferred
Broad-billed Parrot = <b>Raven Parrot</b> <i>Lophopsittacus mauritianus</i>	?WF/ ?C?B	?1670s [<1695]	“probably disappeared as a result of hunting, deforestation & nest predation by introduced monkeys & rats”	nest-robbing by monkeys, old birds surviving long after reproduction had ceased; deforestation was minimal at the time, and no-one reported hunting this species.
<b>Mauritius Lizard-owl</b> <i>Mascarenotus sauzieri</i>	N/pC	c.1840 [<1859]	“probably due to an increase in deforestation ... had survived alongside introduced predators for centuries”	as left + deforestation removing nest sites & near extinction of forest skinks (putative prey). Desjardins in 1837 (in C&H <sup>12</sup> ) also invoked “the large number of poachers who roam the woods that remain”
<b>Réunion Lizard-owl</b> <i>M.grucheti</i>	N/pC	[unknown; H&W suggest “some time in the 1700s”]	“severe deforestation”	not specified as absolutely no data [this species was never observed alive, so may not have been around in human times, or could have succumbed before 1700 to rats; probably disappeared long before any severe deforestation]
<b>Rodrigues Lizard-owl</b> <i>M.murivorus</i>	N/pC	1726-1761	“probably as a result of severe deforestation caused by tortoise hunters burning off the vegetation”	timing suggests cats; survived rats; there was no deforestation, and prey was still abundant.
<b>Rodrigues Bulbul</b> <i>Hypsipetes</i> sp. [undescribed]	N/A	[unknown]	[not included]	Not reported by visitors, may have been exterminated by rats before Leguat arrived in 1691

<sup>12</sup> Wrongly cited as a quote from Clark (1859) in H&W

	site	Extinction	Cause in Hume & Walters	Cause inferred
Réunion Crested Starling = <b>Hoopoe Starling</b> <i>Fregilupus varius</i>	N/pC	1850s [<1860]	disease or parasite, aided by replacement of coffee by sugar, and deforestation of the 'cirques'	as left
<b>Rodrigues Starling</b> <i>Necropsar rodericanus</i>	N/pC	1726-1761	"the islets provided the only refuge, but when rats eventually colonised them, the bird's fate was sealed"	confined by rats to islets by 1726; cats blamed, but #rat colonisation of islets perhaps more likely (cf. pigeons).
<b>Réunion Fody</b> <i>Foudia delloni</i>	N/A	?1675-80	"likely that the population crashed once these vermin [Ship Rats] had become established"	as left; the only observations precede the arrival of rats.

## A Plastic Survey of Blue Bay and Pointe D'Esny, Mauritius

Graham Shelbourne & Nicholas Ray  
Nottingham Trent University,  
School of Animal, Rural & Environmental Sciences,  
Burton Street, Nottingham, NG1 4BU, U.K.  
[[graham.shelbourne@ntu.ac.uk](mailto:graham.shelbourne@ntu.ac.uk)]

**Abstract:** Plastic waste, in particular neustonic waste poses a threat to wildlife. Blue Bay is situated on the south east coast of Mauritius and is a 20km<sup>2</sup> shallow lagoon with a fringing reef and a number of islets. It includes an area designated a marine park in 2000. The lagoon contains 38 species of coral and 125 species of fish. The outer reef protects the island from incoming neustonic plastic fragments creating an opportunity to identify anthropogenic debris from the mainland. Beach surveys and tropical forest surveys used finger-tip searches to a depth of 2cm whereas as underwater surveys used quadrats and the roving diver technique. 28 transects and quadrats were surveyed in total over a 2 week period (March/April 2012). The fragments were analysed using the Resin Identification Code. The results indicate 1 beach location with higher levels of plastic fragments. These represent a threat to the local wildlife primarily through ingestion. Protected areas including the marine park and Ille Aux Aigrette show low levels of plastic debris.

### Introduction

Plastic (synthetic polymer) debris is known to be a global threat to our oceans (Derraik 2002, Moore, 2008 & Cole *et al* 2011). Its qualities of lightness and durability are both a benefit and a cost (Ryan *et al* 2009). Neustonic waste has been extensively demonstrated to be a serious threat to marine life (Fowler 1987; Ryan 1987; Bjorndal *et al* 1994; Moore *et al* 2001). Further evidence was obtained from the North Western Mediterranean Sea by Collignon *et al* (2012) and together with numerous other studies (Shiber 1979, Cadee 2002 & Otley & Ingham 2003) confirmed it as a global issue. Human discards have resulted in a serious threat to marine life. Bugoni *et al* 2001 reported that 13.2% of dead green turtles (*Chelonia midas*) examined in Rio Grande de Sul in Brazil died as a result of plastic debris ingestion and a further 13.6% died as a result of fishing activities. Neustonic waste has further been shown to act as a breeding ground for some species which seek refuge on this material and travel on currents around the oceans (Gutow & Frank 2003) ultimately providing a vehicle for invasive species. According to Barnes (2002) human litter doubles the opportunities for rafting biota. Neustonic waste was predicted by Day *et al* (1988) to become a threat to human health where they entered the food chain. Swan (2008) showed that phthalates have an anti-androgenic effect on human reproduction. Furthermore exposure to phthalate esters have been shown to produce abnormal reproductive development in male rats (Howdeshell *et al* 2008) and bio-persistent organic pollutants (POPs,) shown by Mato *et al* 2001 and Rios *et al* (2007) to adhere to plastic debris, have been shown to reduce sperm chromatin integrity in Intuits (Bonde *et al* 2008). These POPs include polychlorinated biphenyl (PCBs) known to cause cancer in animals and may do so in humans (Endo 2005). It is with these issues in mind that this study was undertaken.



Pointe D'Esny, Mauritius has a fringing reef system encompassing an area of approximately 20km<sup>2</sup>. This includes a MPA of 353ha managed by the Albion Ministry of Fisheries Research Centre. The bay is therefore protected from the immigration of neustonic plastic by the reef structures and the turbidity of the pelagic ocean. With a human population in 2005 of 1.2 million this is expected to increase to 1.41 million by 2020 (Richmond 2011) increasing the pressure on marine resources. Potential sources of plastic debris are the mainland of Mauritius or enclosed islands or the Indian Ocean Gyres. The area was subjected to a range of destructive processes in the 20<sup>th</sup> century including overfishing, mechanical or chemical destruction of the reef and non-recycled discharge (Lagon Bleu 2012). Mahebourg is the local fishing centre (Expedition Tour 2012) with a strong tradition of artisanal fishing and an active fish market where tangs, parrot fish and wrasse caught in the lagoon have been photographed for sale.

Ile aux Aigrette is located in the lagoon approximately 800 metres from the mainland (Lat 20°25'13.45"S Long 57°43'58.88"E) and is a coralline island subject to restoration by Mauritian Wildlife Foundation. The island is divided into 1624 permanent quadrats (12.5 x 12.5 metres) identified by posts in the ground. A parallel project facilitated the acquisition of plastics data.

This study aimed to ascertain the levels and nature of plastic debris in the lagoon of Pointe D'Esny (from Latitude 20°27'17.82"S/Longitude 57°41'58.87"E to Latitude 20°23'39.84"S/Longitude 57°45'14.98"E). Objectives were identified as clarifying the quantity of plastic debris, the nature of that debris and to locate specific areas subject to the highest density. Additionally analysis of the debris was intended to ascertain if particular types of plastic could have a common source.

The Republic of Mauritius web-site (2012) lists five companies registered for recycling plastic which are Polypet Recyclers Ltd, DKD Co Ltd, Philip Polybag Manufacturer Co. Ltd, Plaspak Group and Viper Transport & Co Ltd.

## **Methodology**

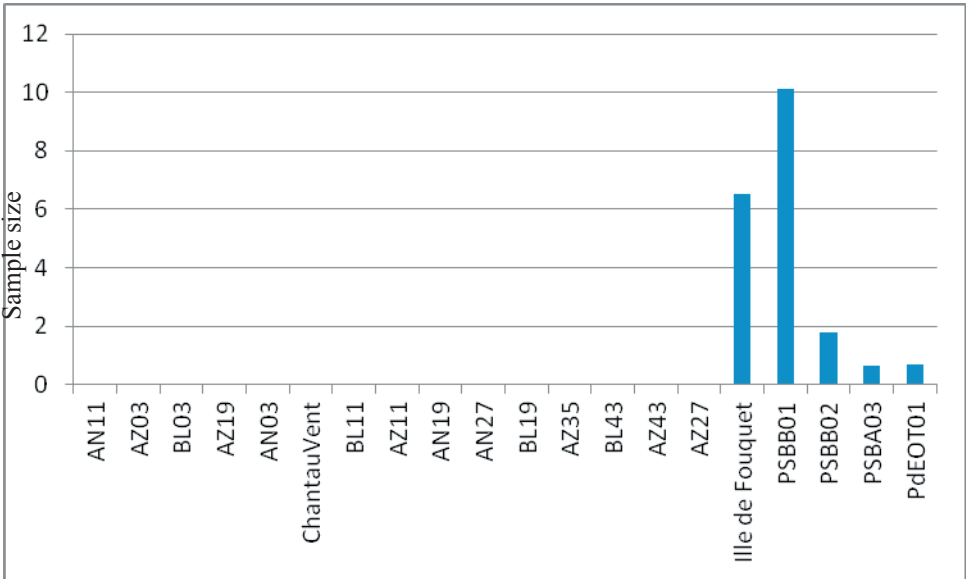
A review of methods by Rees & Pond (1995) and a further study by Velandier & Mocogni (1999) proved valuable in choosing effective methods appropriate to a range of environments from public beaches, tropical coastal forest and 20 metre deep dive sites. Most of the reviewed methods were constrained by solo investigation. This study had 14 Nottingham Trent University undergraduates completing data collection. Beach surveys and tropical forest surveys used finger-tip searches to a depth of 2cm whereas as underwater surveys used line transects and the roving diver technique (Schmitt *et al.* 2002). In order to obtain useful data measurements were equated to fragments per m<sup>2</sup>. Araujo *et al* (2006) demonstrated that the most effective areas to be targeted for sample collection covered a 15 metre width of the littoral zone above the high tide mark and this was the approach selected. Ryan *et al* (2009), following a review of methods, recommended to The United Nations Environment Programme (UNEP) suggests that standing stock surveys should cover 50m distances although they subsequently suggested 100m. Due to local anthropogenic topography these surveys were conducted over 30m transects. Where variations occurred as a result of vegetation these areas were also searched. Where man-made structures were present the loss of search area

was compensated for in the estimation of fragments per m<sup>2</sup>. 27 transects and quadrats were surveyed in total over a 2 week period (March/April 2012). The fragments themselves were identified using the Resin Identification Code (American Chemistry Council 2011) and results recorded in the field using Microsoft Excel. This method was selected in order to ascertain where plastic types were appropriate for recycling and is globally the industry standard. This was possible with land based collection but where roving diver techniques were employed underwater this was not possible. Results for these are therefore dealt with separately. The range sites are identified as follows: 14 quadrats on IAA, 5 dive sites, 4 beach quadrats, 3 Snorkelling quadrats and 1 quadrat on outlying island (Ile de Fouquet, Lat 20°23'44.33"S – Long 57°46'36.37"E). One site was repeated to check the validity of the method and results were congruent.

Underwater areas searched by scuba diving concentrated on 2 dive sites, each repeated in order to provide an estimate of the accuracy by comparing data. Recovery was also restricted in line with standard safety protocols.

**Results**

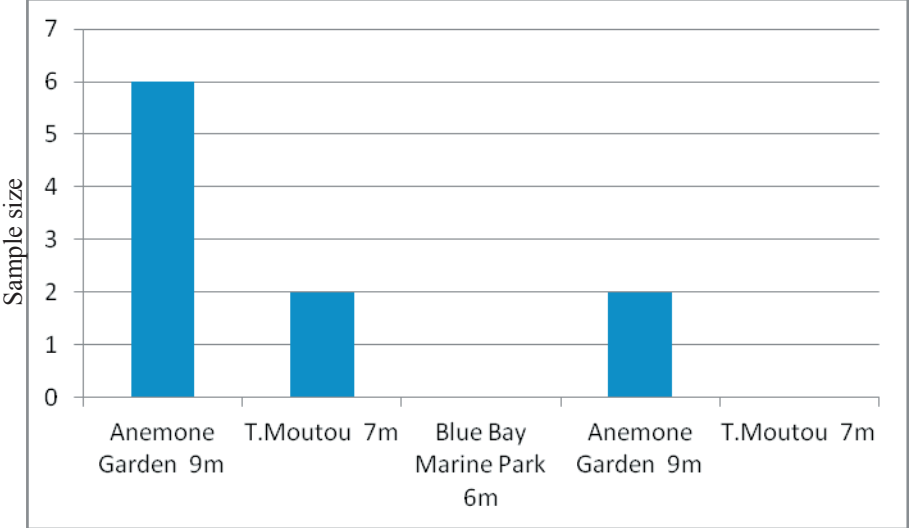
The results show that all mainland sites tested (4) were found to contain varying amounts of debris and this was heaviest in the areas of the public beaches. Deeper areas of the lagoon lower levels of debris and a national reserve established on Ile aux Aigrette had even less (courtesy of the Mauritian Wildlife Foundation). In total 27 sites were sampled (one repeated) over a two week period. Fig.1 shows the quantities of plastic collected from each area.



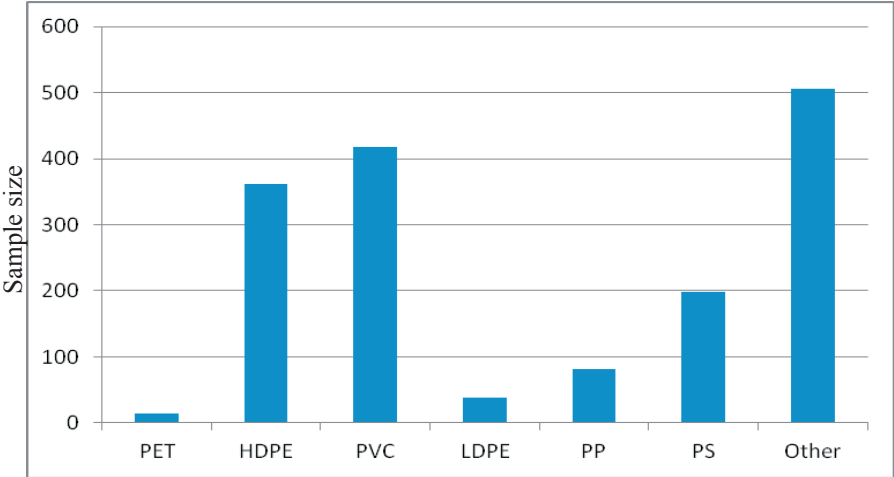
**Fig.1** Plastic debris quantities over survey areas.

These results identified very specific areas where deposition was high and these finding will be discussed later in this paper. Fig.2 shows the results from the underwater surveys using the roving diver technique, demonstrating considerable differences on repeated dives although this may be disproportionate as a result of the relatively low quantities found.

As well as the quantity of fragments collected the types were also identified and can be seen in Fig.3. These data may identify where recycling potential exists for comparison with available resources on the island.



**Fig. 2** Data collected by scuba diving using the roving diver technique.



**Fig.3** Analysis of data collected by plastic type across all sites.

## Discussion

The levels of plastic debris appear to be relatively low around the lagoon with two specific exceptions. Ile de Fouquet is an outlying island located within the lagoon and despite an absence of facilities, jetty or toilets. It is very popular with locals for picnics and family celebrations. As a result large amounts of detritus can be found on the island with a limited waste collection service. The location is susceptible to strong winds and there is therefore a high potential for debris to be deposited in the surrounding marine environment. Ad-lib observations at the time recorded high numbers of visitors and overflowing rubbish bins with material piled up next to the bins. This indicates that many visitors seek to place their waste in an appropriate area assuming it will be collected. *Ergo* either visitors need to remove their own waste or provision needs to be made for its collection. Of particular concern is the presence of nesting areas for *Phaethon lepturus*. It is a surface plunging bird taking fish and squid but may be vulnerable to ingestion of neustonic waste. The island is home to a number of reptile species, some of which are endangered or vulnerable.

The most substantial amount of debris was found at PSBB01 (Lat 20°26'33.71"S – Long 57°42'46.59"E) which was a transect on the public beach. This location was randomly selected and from a length of public beach popular with the locals, particularly on Sundays. This survey was completed on a Monday and indicative of debris left overnight. It would have been useful to categorise the types of items to identify if there were opportunities to target future items for recycling. This should be considered with future studies. Items that were specifically identified included baler twine, glow sticks (used by locals at night) and flip-flop shoes. It was noticeable that there was a virtual complete absence of drink bottles. This may be as a result of a recycling scheme which, on this evidence would seem to be very effective.

A second section of the public beach surveyed was adjacent to a jetty (Lat 20°26'39.16"S- Long 57°42'59.82"E) where tourists boats moored and hence attracted a lot of visitors. It may therefore be considered surprising, not that levels were high, but in fact they were lower than anticipated. Local skippers reported that one reason for this was that their crews did a certain amount of cleaning of the area themselves.

The results for the roving diver collections were more complex. It is worth stating that the quantity of plastic collected was low in comparison to land transects, however these results are constrained considerably by the environment. Undoubtedly the data would have been more reliable had underwater transects been laid in a more traditional manner. This method was used with some snorkelling surveys in shallow water where surface GPS could accurately confirm the location. The roving diver technique does allow for the gathering of evidence but is unlikely to be consistent on repeat dives and would make year on year comparisons difficult. The location is difficult to accurately identify and may require the use of permanent markers of some kind. This practice is prohibited by the Albion Research Centre in order to protect the lagoon. Representation will need to be made in the light of this study to see if this can be agreed. These would also facilitate parallel studies on biodiversity and abundance. Alternatively more repeated dives would provide better data. This review needs to be completed prior to further surveys being undertaken.

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# Biogeography of the terrestrial and freshwater biota of the Seychelles islands

Justin Gerlach

133 Cherry Hinton Road, Cambridge CB1 7BX, U.K.

*gerlachs@btinternet.com*

**Abstract:** The biodiversity of the Seychelles islands has long been considered to include a notable component of species isolated on the islands following the final fragmentation of Gondwanaland 65 million years ago. A review of the biogeography of all non-marine multicellular organisms recorded on the 115 islands is presented. The southern coral atolls of the group have a small biota descended from colonists arriving on the atolls as a result of rafting, mainly from Madagascar and Africa. A much smaller dispersive element is also present in the granitic islands, but these include fewer species of African origin. Few species can be confidently identified as having a Gondwanan origin. Detailed molecular phylogenetic studies are needed for a wide range of taxa to evaluate the true origins of the biota of these interesting islands.

Biogeographical patterns have long been of interest as indicators of past distributions and evolutionary processes. Wallace (1880) first drew attention to the extreme significance of islands as exemplars of biodiversity and since then they have been the subject of intense study at multiple levels. These include distribution patterns as indicators of dispersal or vicariance processes, and equilibrium dynamics as described by Island Biogeography Theory (McArthur & Wilson 1967). In all studies of island biogeography it is apparent that different organisms have different dispersal mechanisms which dramatically alter their biogeography. Highly motile species such as flies or birds tend to have relatively low endemic diversity levels and wider ranges except on the most isolated of islands. This often makes them less useful in biogeographic studies than less motile groups such as amphibians and molluscs. These latter two groups are of particular significance due to their relatively limited dispersal abilities over large areas of ocean.

High levels of endemism in the amphibian fauna of the Seychelles islands (90%) was one of the early pieces of evidence indicating an ancient continental origin for the islands (Wallace 1880). However, the low diversity of the group (only 12 species in the islands) and the restriction of most species to four islands (50% restricted to two islands) makes detailed biogeographical analysis impossible. The biogeography of Seychelles molluscs also has a long history, being mentioned by Wallace (1880) and Gardiner (1936). However, the first serious consideration of their biogeography was given by Bruggen (1967, 1986) who discussed the affinities of the Aldabran Streptaxidae. He noted the short geological history of the atoll and the close affinity of the streptaxids to African species, with a greater Asian influence in the granitic islands. Peake (1971) gave some examples of biogeographical patterns in molluscs but these were based only on literature and include several misidentifications. He considered the origin of the fauna to be primarily due to dispersal, accounting for the widely distributed coral island species but also the endemic genera such as *Stylodonta*, more usually

considered to be Gondwana relics. Gerlach & Bruggen (1999) noted that the mollusc fauna could be divided into two groups: the widespread recent colonists (introductions, cosmopolitan species and colonists from Africa) predominant in the low-lying coral atolls and cays and the more ancient species (largely of Gondwanan origin) of the high islands. The biogeography of only one genus has been analysed in detail within the islands; the cerastuid *Pachnodus* (Gerlach 1999). This genus is a Gondwanaland relict and shows a largely vicariant pattern with diversity being promoted by isolation and habitat specialisation.

In the 20<sup>th</sup> century other groups received some consideration (insects in general – Scott 1936; Cogan 1984), plants (Summerhayes 1931) and lizards (Cheke 1984). These studies concluded that oriental affinities dominated for the plants (Christensen 1912; Summerhayes 1931) in the granitic islands but with a higher pantropical or Indo-Pacific component in the coral islands (Procter 1984). Similarly, granitic Seychelles insects have been largely considered to be oriental (Holdhaus 1928; Scott 1933), as have the land snails (Nevill 1869).

In investigating the origins of taxa based simply on distributions particular problems are found in distinguishing indigenous species from invasive ones. The difficulty of distinguishing successful colonist from invasives is exemplified by the nemertean ribbon worm *Geonemertes pelaensis*. This species was first described from south-east Asia (1863), followed by Seychelles (1905) and the west Pacific (1927). Records from other localities are more recent: Mascarenes (1975) and Caribbean and Florida (1982), suggesting a recent range expansion from an originally Indo-Pacific distribution. Caribbean populations can be considered introductions based on dating and biogeography, but its natural distribution within the Indo-Pacific remains conjectural. It is noteworthy that the only other members of the genus are the extinct Mascarene *G. rodericana* and the Phillipine species *G. philippinensis*.

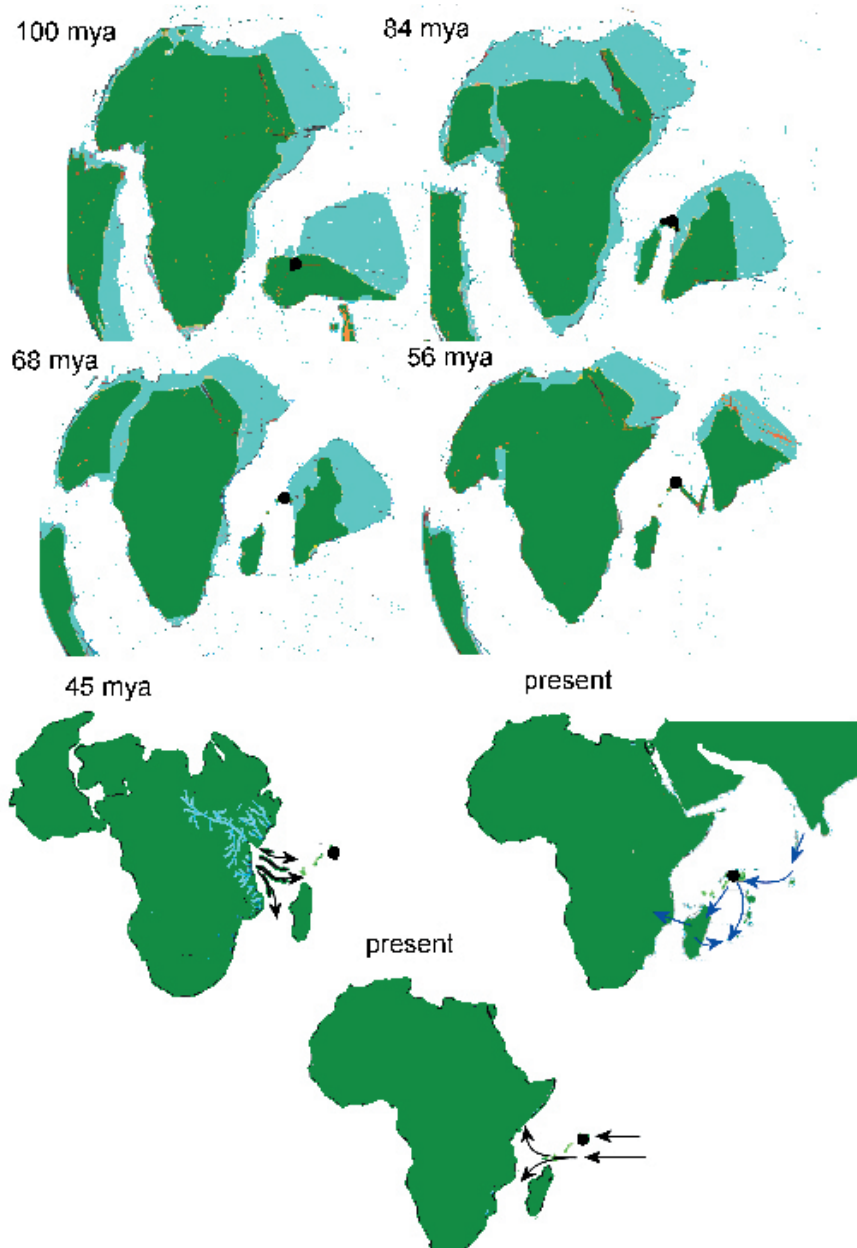
In the past 10 years there has been a significant increase in biogeographical research, particularly using molecular techniques e.g. (Rocha *et al.* 2010a-d, 2011, 2013; Lima *et al.* 2013; Rouhan *et al.* 2007; Townsend *et al.* 2010). Western Indian Ocean biogeography studies were synthesised by Agnarrson & Kuntner (2012). In this synthesis they erroneously claimed that most of the granitic Seychelles islands had been submerged at times and that the biota was therefore largely of dispersive origin. They cited in support of this the fact that freshwater crabs had colonised by transoceanic dispersal (Daniels *et al.* 2006; Cumberlidge 2008; Daniels 2011) but noted that this did not apply to caecilians (Zhang & Wake 2009), sooglossid frogs (Biju & Bossuyt 2003) and some ferns (Lehtonen *et al.* 2010). This apparent contradiction was not resolved. A more detailed synthesis is presented here specifically for the Seychelles islands.

## Geological background

The origin of the Seychelles islands as a whole is well established following numerous studies of Madagascar-Seychelles-India ('Greater India') geology. The islands are a remnant of the progressive fragmentation of Gondwanaland starting some 180 million years ago (mya). 100-90 mya Greater India split from Africa, followed by the movement of India-Seychelles and the Mascarene Plateau northwards, away from



**Fig. 1.** Position of Seychelles relative to nearby landmasses over the past 100 million years (after Ali & Aitchison 2008), and present day position with 100 m lower sea levels showing island stepping-stones scenario – blue arrows (after Warren *et al.* 2010), and prevailing ocean currents – black arrows.



Madagascar 89-85 mya (Storey *et al.* 1995). There is a recent suggestion that Mauritius overlies a fragment of ancient continent, being called 'Mauritia' (Torsvik *et al.* 2013). This appears to have broken off from the Madagascan part of Greater India, and to have been isolated from around 70 mya.

At this time extensive areas of magma surfaced to the east of Madagascar, giving rise to the Mascarene Ridge (Mukhopadhyay *et al.* 2012). Seychelles can first be considered to have existed 62 mya when the Seychelles microcontinent split from India as a result of intense activity in the Carlsberg ridge which started 64 mya (Mukhopadhyay *et al.* 2012). This suggests that Gondwanan affinities may be found in taxa showing a close relationship to India, Madagascar and, to a much lesser extent, Africa.

64 mya the area that became the Seychelles microcontinent would probably have been volcanically active, with traces of such activity on Silhouette and North islands. A large part of the microcontinent was, however, probably stable and volcanic activity may have been geographically very restricted. There is no evidence of volcanic activity on the Seychelles microcontinent (or plateau) since that date. Volcanic activity probably occurred to the south-west of the microcontinent, giving rise to the Amirantes and southern atolls. Whether these were ever exposed volcanoes or remained submarine sea mounts is not known. The coral islands have been dated back to 2.5 mya (in the case of Aldabra) but have been submerged repeatedly since then, most recently 125,000 years ago (Braithwaite *et al.* 1973).

Between 50 mya and the Ice Ages of the past 5 million years the land-masses in the Seychelles area would have been subject to erosive process and subsidence as the Amirante trench formed by subduction (Mukhopadhyay *et al.* 2012). The original topography of the Seychelles microcontinent is unknown; by the start of the Ice Ages it may have been similar to the present day and principally affected by fluctuating sea levels.

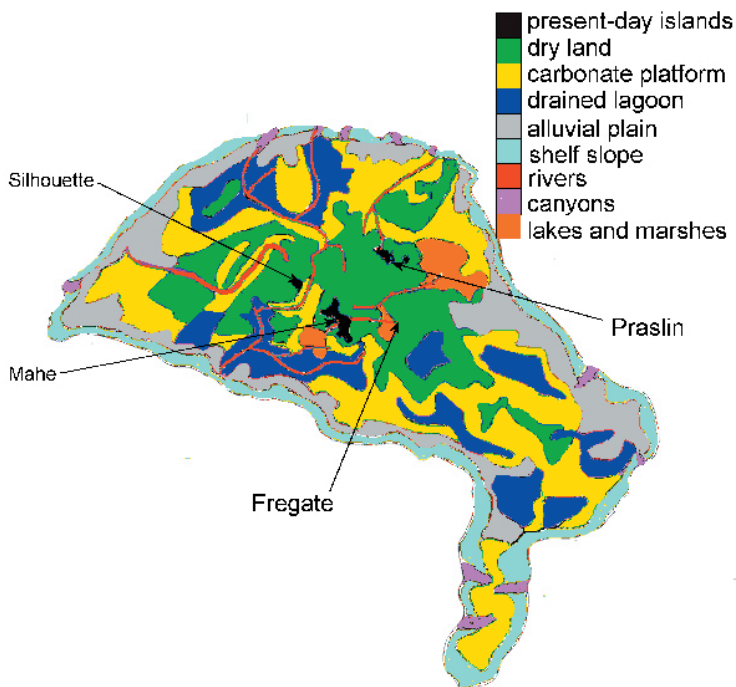
During the Ice Ages the Seychelles Bank would have been subject to repeated periods of exposure and extensive submergence. At times of extreme low sea-level all of the Bank would have been exposed as largely dry land. Lowland organisms would have been able to spread across much of this area, and at least some of the higher altitude species. Conversely, during high sea-levels the lowlands would have been flooded, isolating species on separate islands, drastically reducing the area of some of today's islands and completely flooding the lower ones. At the same time the coral islands of the Amirantes and the southern atolls, and the Salha de Maya bank would have been repeatedly exposed and completely submerged.

There are no detailed reconstructions of the exposed Seychelles Bank but a crude interpretation of a variety of data sources was carried out in 1986 (Badyukov *et al.* 1988). This is simplified here (Fig. 2), showing the unification of the islands by dry land at extreme low sea levels. There would have been rivers creating partial barriers between Silhouette, Fregate and the other islands.

## **Dispersal routes**

The isolation of the islands as indicated by the geological reconstructions may not have been incomplete as chains of islands may have allowed some organisms

**Fig. 2** Reconstruction of the main habitats of the exposed Seychelles plateau (modified from Badyukov *et al.* 1988). Black – present day islands; green – dry land; yellow – sea-level plateau of exposed carbonate platform; blue – tidal lagoon and estuaries; pale green - marsh; grey – reef rim, tidally exposed; pale blue – reef



to move between the apparently isolated land masses. These island chains have been described as the “Lemurian stepping-stones” (Schatz 1996; Steenis 1962) and are supposed to have been created by a drop in global sea levels 56-34mya exposing the Seychelles bank and Mascarene plateau (Rage 2003).

Ocean currents may have been favourable for colonisation from Africa to Madagascar and the Seychelle microcontinent initially until 50 mya (Masters *et al.* 2006), or occasionally until 20 mya (Ali & Huber 2010). Since then present-day current patterns have predominated, with a general east-west transport. This makes oceanic dispersal from Asia to Seychelles and from Seychelles towards northern Madagascar and east Africa most likely. Local current patterns around Aldabra are predominantly from the direction of Madagascar. It has been hypothesized that during periods of extreme low sea levels the exposure of the Seychelles Bank and the Mascarene Plateau would have altered the currents, specifically by blocking most of the east-west currents. This may have facilitated movement of organisms in a reverse direction, from Madagascar north-eastwards along the Amirante chain, which would have been exposed as a chain of stepping-stones up to the Seychelles Bank.

**Lemurian stepping stones**

The putative colonisation route between Africa/Madagascar and Asia via Seychelles was termed the ‘Lemurian stepping-stones’ by Van Steenis (1962) who proposed that a land-bridge (‘Lemuria’) had existed between Madagascar and Sri Lanka. Schatz (1996) proposed that Seychelles or the Mascarenes may have acted as these stepping stones.

Van Steenis (1962) included *Pyrostria* in the Rubiaceae as an example of a genus that used this route in the Eocene-Oligocene. However, a recent phylogeny of the Vanguerieae (Rubiaceae) (Wikstrom *et al.* 2010) failed to support this route, with no evidence of progression from Asia to Africa, via the Indian Ocean.

**Broad geographical patterns**

The comprehensive enumeration of the biodiversity of the islands (Table 1) shows that different taxonomic groups show differing broad geographical patterns (Fig. 3). These differ too much to allow any broad generalisations to be made. Even within major taxonomic groups there are notable differences, such as in the Myriapoda where the Diplopoda (millipedes) are Pantropical (60%) or Western Indian Ocean

**Table 1.** Numbers of species of different taxonomic groups identified in the Seychelles islands. Note Fungi and Nematoda are still insufficiently investigated and that Bryophyta collections have not been completely identified. Number of angiosperms are restricted to species established in the wild, excluding cultivated species.

	endemic	indigenous	introduced	uncertain	total
Lichens	0	305	0	100	405
Fungi	0	11	0	0	405
Bryophyta	14	161	0	0	175
Pteridophyta	17	66	7	2	92
Angiospermae	109	533	873	119	1,634
Platyhelminthes	2	0	7	9	18
Nematoda	18	20	1	12	54
Nemertea	0	0	0	1	1
Rotifera	0	0	0	36	36
Annelida	4	1	9	0	14
Mollusca	51	1	13	1	89
Tardigrada	19	14	0	0	33
Crustacea	24	48	4	4	82
Hexapoda	1,606	1,366	126	33	3,081
Chelicerata	201	127	16	15	359
Myriapoda	40	35	4	10	88
Vertebrates	54	39	24	3	120
TOTAL	2,169	2,727	1,084	345	6,586

(20%), whereas the Chilopoda (centipedes) are Asian (45%) or African (19%). The current estimates of origins for angiosperms are 14-35% endemic depending on what proportion of species are considered to be native. Procter (1984) considered the affinities to be mainly Asian but gave no comprehensive analysis for this. Scott (1933) considered 57% of the 2,426 species known at the time to be endemic and considered the majority to have affinities in the Oriental zoogeographical region. In Cogan's (1984) review the number of species was estimated to be 3,500 and from a selected group (Phasmopeta, Dermaptera, Blattidae, Odonmata and some Diptera) 51% were thought to be endemic, and the non-endemics predominately Afrotropical, followed by Oriental. The present analysis also gives 51% endemism for a total of 3,120 species and 25% of non-endemics are thought to be African in origin and only 13% Oriental.

Fungi have not been adequately sampled, the more inconspicuous forms in particular have been rarely studied (e.g. Sparrow 1975; Tedersoo *et al.* 2007; Suvi *et al.* 2010; Piątek & Vánky 2012) only one paper on macrofungi has been published (Watling & Seaward 2004). Lichens have been more extensively studied although new records are still being made (Sipman 2010).

The flying vertebrates (birds and mammals) have very high Western Indian Ocean affinities, with a strong Asian connection in the birds; it has been proposed that Seychelles acted as a steppingstone in the colonisation of Madagascar by Asian birds (Warren *et al.* 2005).

Comparison of the diversity of taxa with different biogeographical origins and their ranges shows that the southern atolls are occupied exclusively by recent colonists (in accordance with the islands having been exposed for only 120,000 years), with the majority from Madagascar (55% of native snail species). The granitic islands support a mainly ancient fauna (67% for snails: 44% having Gondwana affinities, 23% Asian possibly reflecting continental drift), although there is also a significant proportion of recent colonists from the Malagasy region (21% of snails). The dominance of the Malagasy origin within the recent colonists is more apparent in the granitic islands than in the coral islands (69% of snails compared to 55%). Most ancient taxa have smaller ranges than those of recent origin.

### **Vicariance or dispersal: the evidence**

Table 2 summarises the studies that have discussed the origins of the Seychelles fauna and flora. In the molecular studies a molecular clock has sometimes been used to provide dating estimate. This is based on the assumption that the mutation rate within the genes studied remain constant, this mutation rate should be calibrated to the phylogeny produced, which requires some accurately dated points. Such calibration points are very rare, for the Western Indian Ocean the dating of emergence of the volcanic islands provide maximum ages for some lineages and these have been used in some studies (e.g. Warren *et al.* 2005). Studies that use assumed rates of mutation, without calibration should be considered cautiously (see Heads 2005 for a detailed criticism of examples of the use of uncalibrated clocks).

**Table 2.** Origins of genera and families in Seychelles. Dating is noted as E – estimate, C – calculated, (c) – calculated but without independent calibration.

<b>Taxon</b>	<b>Origin</b>	<b>Route</b>	<b>Date (mya)</b>	<b>Data type</b>	<b>Source</b>
Pteridophyta	<i>Nesolindsaea</i>				
	<i>Elaphoglossum</i>	long-range dispersal		molecular	Rouhan <i>et al.</i> 2004
Palmeae	<i>Deckenia</i>				Baker <i>et al.</i> 2011
	<i>Lodoicea</i>	vicariant			Baker <i>et al.</i> 2011
	Versafflettiinae				
	( <i>Roscheria</i> + <i>Verschaffeltia</i> , <i>Nephrosperma</i> + <i>Phoenicophorium</i> )	long-range dispersal			Baker <i>et al.</i> 2011
Araceae	<i>Pistia</i>	vicariant			Renner & Zhang 2004
Medusagynaceae	<i>Medusagyne</i>				Fay <i>et al.</i> 1996
Dipterocarpaceae	<i>Vatieropsis</i>		25 C - but ancestor in Greater India early Eocene		Gunasekara 2004; Gamage <i>et al.</i> 2006
	<i>Nepenthes</i>	vicariant			Danser 1928; Clarke 1997
Rubiaceae	<i>Ixora</i> ( <i>Pavettoides</i> )	land bridges		morphology	Meimberg <i>et al.</i> 2001
	<i>Ixora</i> ( <i>Microixora</i> )				B r e m e k a m p 1937b; Smith & Darwin 1988; De Block 1998
Araliaceae	<i>Pyrostria bibracteata</i>				Wikstrom <i>et al.</i> 2010
	<i>Canthium carinatum</i>				Wikstrom <i>et al.</i> 2010
	<i>Polyscias</i>	vicariant			Lowry & Plunkett 2010
				molecular	

<b>Taxon</b>		<b>Origin</b>	<b>Route</b>	<b>Date (mya)</b>	<b>Data type</b>	<b>Source</b>
Annelida - Haemadipsidae	terrestrial leeches ( <i>Idiobdella</i> and <i>Mahebdella</i> spp.)	Post-Gondwanan relics, closest to Madagascar	vicariant		morphology	Borda <i>et al.</i> 2007
Annelida - Oligocha	<i>Maheina</i>	Gondwana?, endemic Madagascar ?	?		morphology	
Mollusca - Pomatissidae	<i>Tropidophora pulchra</i>	Asia ?			morphology	
Mollusca - Hydrobiidae	<i>Moominia willii</i>	Gondwana	vicariant		morphology	
Mollusca - Acavidae	<i>Sylodonta</i>	Gondwana (west Africa)	vicariant		morphology, molecular	Mordan 1991, 1992 Bruggen 1975, 1978; Gerlach & Bruggen 1999)
Mollusca - Cerastidae	<i>Pachnodus</i>	Gondwana	vicariant		morphology	Rowson et al. 2011
	A) <i>Augustula</i>	molecular phylogeny origin ?	dispersal ?	C - Early Tertiary ?	molecular	Rowson et al. 2011
	B) <i>Priodiscus</i>	Molecular Origin ?	dispersal ?	C - Early Tertiary ?	molecular	Rowson et al. 2011
	C) other endemic genera	Mascarenes, origin ?	dispersal ?		molecular	Rowson et al. 2011
Mollusca - Gastrodon- toidea	<i>Nesokaliella</i>	basal		ancient ?	morphology	Gerlach 2001a
Crustacea - Talitridae	<i>Talitroides</i>	Greater India or alien?	?		morphology	Bousfield 1984
	<i>Syecheillum</i>	Africa	dispersal	8.7 (5.8-11.8)	molecular	Daniels 2011
Araneae	<i>Nephila inaurata</i>	Western Indian Ocean				Kuntner & Agnarsson 2011 & Kuntner
	<i>Nephylengys</i>	Western Indian Ocean				Agnarsson 2011 Wesener & Van
Myriapoda	<i>Seychellonema</i>	allied to Thereuopoda from south, east, south-east Asia and Australia	vicariant		morphology	den Spiegel 2009; Butler et al. 2010
Insecta - Drosophilidae	<i>Zaphrotius</i>	Asia to Africa by stepping stones				Yassin et al. 2008
Pisces	<i>Pachypanchax</i>	Madagascar	vicariant		molecular	Hedges et al.
Amphibia - Caeciliidae		Gondwana	vicariant		molecular	
Amphibia - Sooglossidae		Gondwana	dispersal		molecular	
Amphibia - Hyperoliidae	<i>Tachycinemis</i>	Madagascar	(rafting) vicariant?			
Reptilia	<i>Pamelaescincus</i>	Afro-Malagasy				Brandley et al. 2005

<b>Taxon</b>	<b>Origin</b>	<b>Route</b>	<b>Date (mya)</b>	<b>Data type</b>	<b>Source</b>
	<i>Janetaescincus</i>	Afro-Malagasy			Brandley et al. 2005
	<i>Lycognathophis</i>	Ethiopian & Oriental			Dowling 1990;
	<i>Archiaus tigris</i>	Africa	48.5-28.7 C	molecular	Vidal et al. 2008
	<i>Ailuronyx</i>	Afro-Malagasy	Cretaceous ?		Townsend et al. 2011
	<i>Urocyon ledon</i>	Afro-Malagasy	Cretaceous ?		A. Bauer pers. comm.
	<i>Trachylepis</i>	Asian	Cretaceous ?		A. Bauer pers. comm.
	<i>Phelsuma</i>	Africa - Comores	24-48 C		Lima et al. 2013
	<i>Pelusios</i>	Madagascar	30 C		Rocha thesis
	<i>Aldabrachelys</i>	Madagascar		molecular	Fritz et al. 2012
	<i>Zosterops</i>	Madagascar			Gerlach & Riux-Paquette 2013
		Asia			Warren et al. 2006
	<i>Dicrurus</i>	Madagascar	-	molecular, Aldabra as calibration	Pasquet et la. 2007
Aves	<i>Hypsipetes</i>				Warren 2005
	<i>Nectarinia</i>	Africa	1-1.9 C	molecular, calibrated	Warren et al. 2003
	<i>Actoena</i>	Asia			Warren et al. 2010
	<i>Otus insularis</i>	Indo-Malaya, or Africa to Asia	3.6 C		Fuchs et al. 2008
	<i>Pteropus</i>	Asia to Africa to Seychelles			O'Brien et al. 2009
		Madagascar		dispersal	Chan et al. 2011
	<i>Coleura</i>	Madagascar		dispersal	Goodman et al. 2012
Mammalia					



For vicariant Gondwanan origins to be identifiable, the group must have little, or no, ability to cross open ocean. Soft bodied animals lacking waterproofing could be good candidates for this; worms, snails and amphibians being the most likely. Leeches have no waterproofing and would not tolerate contact with salt-water; today they are restricted to the dampest high-forest habitats of Mahé and Silhouette islands. This suggests that they have been present on the islands since their formation and are true Gondwana relics, although no dating has been provided for their separation. The coco-de-mer *Lodoicea maldivica* is found in the otherwise Asian group Corylophoideae. This species has a gigantic seed that cannot undergo oceanic dispersal as a viable seed due to its weight. This lack of dispersal ability and Asian affinity suggests that it is a vicariant relict. Some flying species have been suggested to have Gondwanan origins (e.g. the chironomid midges *Tanytus complanatus*, *Larsia pallidissima*, *Gymnometriocnemus* (G.) *mahensis*, *Smittia megalochirus* and *Lepidopus nigratipes* – Sæther 2004), however, these taxa need more detailed investigation.

Dispersal is strongly indicated in the origin of the tiger chameleon *Archiaus*. The ancestral chameleon is thought to have been carried by a freshwater plume from rivers draining the central eastern African coast (Townsend *et al.* 2011). This drainage and its eastward plume would have facilitated rafting along the eastward ocean current of the Palaeogene (Ali & Huber 2010). This outflow would have remained effective until the Mioocene East African rifting forced the rivers into the Nile drainage, northwards.

Vences *et al.* (2003) considered the tree-frog *Tachycnemis* to fall into the group of recent dispersers, in this case from Madagascar although they did not estimate a date for this. However, Heads (2005) criticised the assumptions of their explanation, suggesting that a vicariant origin might be possible.

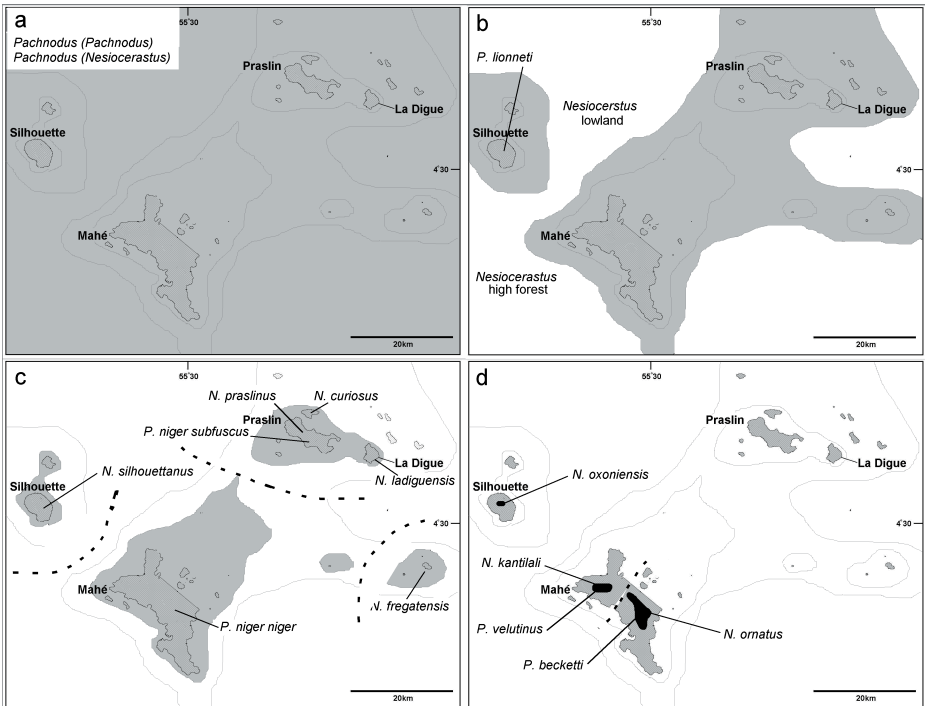
Probable recent colonists include *Hemidactylus mercatorius* with an endemic genetic group in the southern atolls, where colonisation must have occurred since the islands emerged from the sea 100,000 years ago.

The difficulty of determining origins is exemplified by the Streptaxidae family of carnivorous snails. Three lineages are present in the granitic islands of Seychelles, these all diverged during a major radiation of the family coincidental with the fragmentation of Gondwanaland. The dating for the relevant points is too imprecise to determine whether the groups diverged before or after the fragmentation of Greater India, it is therefore unclear whether they originated vicariantly or by early dispersal. The main Seychelles radiation forms a sister-group to the Mascarene streptaxid genera which may indicate that members of this group were distributed across the Mascarene plateau linking Seychelles and the Mascarenes. A major part of the plateau is the Sala de Maya bank which when it was formed some 31 million years ago would have been a substantial island close to, or linked to, the Seychelles plateau. The bank would have eroded progressively over millions of years but may have been in existence until sea-level rise some 10,000 years ago would have flooded it. This leaves several million years for Seychelles streptaxids to colonise the shrinking island before rafting between the islands of the Mascarene group.

## Diversification within the islands

Within the islands the Cerastuidae *Pachnodus* snails show a clear vicariance pattern to speciation, with initial divergence into sympatric subgenera (*Pachnodus* and *Nesiocerastus*) and allopatric speciation of populations isolated on different islands as a result of post-glacial sea-level rise, with some degree of habitat specialisation leading to further speciation (Gerlach 1999). This analysis predates the discovery of the extinct species *P. curiosus*. Inclusion of this poorly known species into the phylogeny places it at the same node as *P. ladiguensis*, which is plausible biogeographically (Fig. 3). This study does not include any dating, studies of which are restricted to the reptiles and the endemic freshwater crab *Seychellum alluaudi* (Table 3).

**Fig. 3.** Evolution of *Pachnodus* species showing the possible distribution of forms at different times over the past 250,000 years. Dry land shaded, 50m submarine contours shown. a) 250,000 years ago – two subgenera widely distributed; b) 100,000 years ago – isolation of *P. lionneti* and habitat specialisation within the *Nesiocerastus* subgenus; c) 50,000 years ago – isolation of different island forms; d) present day – isolation of *Pachnodus* forms within Mahé and specialisation of the high altitude *Nesiocerastus* species.



**Table 3.** Dates for division into island groups based on molecular studies of three reptile genera and the crab *Seychellum*. Splits are between the North (Praslin-La Digue) and South (Mahé-Silhouette groups)

Taxon	Split	Date (mya)	Source
<i>Phelsuma</i>	<i>astriata</i> – <i>sundbergi</i> split	6.4 (4.3-8.4) or 4	Rocha <i>et al.</i> 2013
<i>Phelsuma astriata</i>	North-South	0.5	Rocha <i>et al.</i> 2013
<i>Phelsuma sundbergi</i>	North-South	0.5	Rocha <i>et al.</i> 2013
<i>Urocytyledon inexpectata</i>	North-South	6.24 (3.4-13.9)	Rocha <i>et al.</i> 2011
	Within North	1.6	Rocha <i>et al.</i> 2011
	Within South	0.47	Rocha <i>et al.</i> 2011
<i>Seychellum</i>	Silhouette – others	2.73 (1.8-3.8)	Daniels 2011
	Mahé - Praslin	1.18 (0.8-1.7)	Daniels 2011
	Praslin – La Digue	0.41 (0.2-0.6)	Daniels 2011
	Fregate colonised	0.21 (0.1-0.4)	Daniels 2011

In lizards (data from Rocha *et al.* 2011, 2013) speciation appears to have occurred within the past 6 million years, and mostly within the past million years. Where there is geographical separation of species or genetic groups these can be dated to less than 0.8 mya for most species. The exception is *Urocytyledon inexpectata* which shows a north-south division at least 3.4 million years old and also relatively early divergence within those groups. The *Phelsuma* species show much more recent divergence, indicative of extensive dispersal until recently. In this genus *P. astriata* seems to have diverged into northern, southern and Fregate forms simultaneously (with Fregate being most similar to the norther group, but only weakly so). For *Urocytyledon* however, Fregate groups with the southern forms. In the case of the *Mabuya* skinks the ancestral form seems to have diverged more than 0.8 mya, giving rise to northern and southern clades of *M. sechellensis*. The southern clade seems to have hybridised with *M. wrightii* and also to have given rise to the Fregate population, although with some gene flow from the northern population a well and from Fregate to Mahé. Of all the reptiles this genus appears to have dispersed most frequently.

## Synthesis

There thus seem to be four major events in Seychelles biogeography. Firstly the fragmentation of Gondwana as indicated by the vicariant species of Greater India aged around 64 mya. These comprise the caecilians and the sooglossid frogs and probably *Lodoicea*, *Nepenthes* and *Vateriopsis*. The second group are African migrants from the Palaeogene (65-23 mya) when rivers dispersed organisms eastwards, as exemplified by the chameleon and the freshwater crab. The third group dispersed from Asia into Seychelles and on to Madagascar using the stepping stones, the identified species are mainly volant vertebrates: birds and bats (Warren *et al.* 2006, 2010; O'Brien *et al.* 2009). The fourth category colonised from Madagascar by dispersal over the exposed land areas during periods of glaciation, this probably includes many of the lizard species. The exposed Seychelles and Saya de Malha banks would have altered ocean surface currents in the region, facilitating the south-west to north-east dispersal. Since the rise in sea-level 100,000 years ago ocean currents have been predominantly easterly to north-easterly, reducing colonisation potential from nearby land masses.

Within the islands two further events are identifiable: sea-level rise and current

patterns. Vicariant fragmentation has occurred in the granitic islands as the Seychelles bank has been submerged. In general this may be assumed to have been a broadly homogenous land mass, although with notable altitude variation. However, the present day distribution of some species suggests some patchiness of the habitat on the continental fragment. The restriction of *Lodoicea* to Praslin, Curieuse and St. Pierre suggests that the northern fringe was lower-lying, dryer (possibly fire-prone) habitat suited to palm forests, whereas the southern areas may have been wetter, in association with the high mountains of Mahé and Silhouette. In turn this suggests that *Lodoicea* may have originally been spread across the northern fringe, making a historical presence on La Digue probable. Although there is no direct evidence for this the presence of subfossils of the *Lodoicea*-associated snail *Styldonota studeriana* on La Digue suggest that such a distribution is possible. One other aspect of distribution suggests a notable change in habitats: that of the isolated cloud forest adapted species. Mahé and Silhouette share many biogeographical similarities due to the restriction of cloud forest species on the two islands. This is not surprising given their altitudes, but some of these species have very restricted dispersal abilities. Most notable is the terrestrial dytiscid diving beetle *Labourdonnaisia mahensis* which is restricted to the water film between leaves above 650 m altitude. This is flightless and so its presence on the two islands requires either extreme dispersal events, or a continuous area of habitat in the past. Extreme dispersal would require a storm of such intensity that waterlogged *Northea* leaves could be blown from one island to the other, which may seem implausible. Alternatively cloud forest must have been present from Mahé to Silhouette, accounting for the close similarity of the fauna of the two main habitat patches. For this to have eroded away into the present-day relatively deep marine channel between the islands would require a considerable passage of time. A molecular comparison of the Mahé and Silhouette populations is required to give an indication of the timing of the separation of the *Labourdonnaisia* populations. At present these remain unanswerable enigmas.

As the sea-levels rose Silhouette and North would have been isolated first, followed by a three-way split between Mahé, Praslin and Fregate. This is reflected in snail distributions. Ocean current mediated dispersal gives a different pattern with a north – south split, Silhouette now grouping with Mahé. This is reflected in the reptiles in particular. With dispersal Fregate is anomalous, being at the junction of the northern and southern groups, in most cases it falls into the latter. In the case of the crab *Seychellum* it has been proposed that a freshwater plume from Mahé to Fregate allowed colonisation of the island, this could also have transported rafting animals in that direction, around 210,000 years ago (Daniels 2011). It is notable that the reconstruction of the Seychelles bank exposed during low sea levels indicates that a river may have run from central Mahé to a marsh near Fregate island (Fig. 2), providing a dispersal route from Mahé to Fregate. This may make a more plausible colonisation route for *Seychellum* on Fregate.

Within Mahé there are three haplotype clusters in *Seychellum*, corresponding to the south, the north and La Gogue, La Misere and North Mahé, South Mahé (Daniels 2011). This is in agreement with biogeographical analyses of snails which find a division between north and south Mahé in *Edenutlina*, *Pachnodus*, *Nesokaliella* and *Styldonota*

(Gerlach & Bruggen 1999; Gerlach 2001, 2007). In the case of the crab this appears to relate to river drainages, for the snails it has been interpreted to be due to seal-level changes altering habitats around a topographical division in the La Misere area of Mahé. A similar pattern is thought to occur in sooglossid frogs (pers. obs.).

Overall the biogeography of the Seychelles islands shows a mixture of vicariant and dispersal patterns. This is clearest in recently radiating species groups (e.g. some of the snails) and well studied taxa (reptiles and birds). However, the significance of the original Gondwanan component remains largely speculative after 100 years of biogeographical research. This is unlikely to change until a wide range of taxa have been studied in detail using molecular phylogenies with calibrated dating estimates. The author did propose the organisation of a comprehensive molecular phylogenetic research programme with representative coverage of different groups, however, this proposal was rejected by the Seychelles government (D. Dogley *in litt.*) and research on this topic remains restricted to a piecemeal approach relying on the interests of individual researchers.

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## Appendix: Emendations to the Seychelles fauna monographs

Corrected names are shown in bold.

### Mollusca

#### Euconulidae

*Dupontia* sp. = ***Microcystina minima*** (H. Adams, 19867) (Rowson *et al.* 2010).

#### Subulinidae

*Subulina striatella* = ***Striosubulina striatella*** (Rang, 1831)

#### Cerastidae

*Edouardia conulina* = ***Gittenedouardia conulina*** (von Martens, 1869)

### Myriapoda

#### Chilopoda

#### Scutigerae

***Scutigera coleoptera*** Linnaeus, 1758 – introduced: Praslin (K. Joliffe pers. comm.).

### Chelicerata

#### Araneae

*Nephilengys borbonica* Saaristo, 2010 = ***Nephilengys livida*** (Vinson, 1863) removed from synonymy of *N. borbonica* (Kuntner & Agnarsson 2011).

*Aridella bowleri* Saaristo, 2002 = ***Brignolia bowleri*** (Saaristo, 2002) (Platnick *et al.* 2011).

*Lisa trichinalis* (Benoit, 1979) = ***Brignolia trichinalis*** (Benoit, 1979) (Platnick *et al.* 2011), a Mauritian species.

*Matyotia tetraspinosus* Saaristo, 2001 = ***Heteroonops spinimanus*** (Simon, 1891) (Platnick & Dupérré 2009), an introduced pantropical species.

*Pelecinus mahei* Saaristo, 2010 = ***Pelecinus marmoratus*** Simon, 1891 (Platnick *et al.* 2012) a pantropical species.

*Pholcus longiventris* Saaristo, 2010 = ***Uthina luzonica*** Simon, 1893 (Huber 2011).

*Cenemus squamata* Saaristo, 2010 (misidentified) = ***Cenemus lami*** Berry, Beatty & Prószyński, 1997 (Zabka & Waldock, 2012).

*Brignolia cubana* Saaristo, 2010 = ***Brignolia parumpunctata*** (Simon, 1893) (Platnick *et al.* 2011).

*Silhouettella assumptia* Saaristo, 2001 = ***Noidiatella assumptia*** (Saaristo, 2001) Madagascar, Assumption, Farquar.

### Hexapoda

#### Diptera

#### Culicidae (Le Goff *et al.* 2012)

*Aedes seychellensis* = junior synonym of *Aedes (Aedimorphus) albocephalus*

*Culex antennatus* – new record Aldabra

*Culex sunyaniensis* – new record Praslin

## Clusiidae

*Heteromeringia nigrifrons* Lamb, 1914 = *Heteromeringia tephros* Lonsdale & Marshall, 2007

## Cecidomyiidae

*Megommata seychellensis* was recorded on Mahé in 1940 as a species commonly feeding on *Pulvinaria* sp. (Vesey-Fitzgerald 1940, 1941)

## Syrphidae

Figures of Syrphidae (p. 238) were mislabelled and should be: Fig. 12.1a - *Ischiodon aegyptiacus*, 12.1b - *Eristalinus seychellarum*. *Melanostoma annulipes* is not figured.

Two species were omitted:

*Allograpta nasuta* (Macquart, 1842) widespread in Africa and the western Indian Ocean (see [www.syrphidae.com](http://www.syrphidae.com)) and *Syritta nigrofemorata* Macquart - Aldabra 1968 (Lyneborg & Barkemeyer 2005).

## Coleoptera

### Curculionidae

*Cratopus roberti* Galman *et al.*, 2012 – Praslin

*C. griseovittatus* Linell, 1897 = *Cratopus griseovestitus* Linell, 1887. Galman *et al.* 2012 describe several subspecies despite probable movement of this species between islands. *C. g. griseovestitus* is known from the Mahé and Praslin groups and Silhouette. *C. g. northilandensis* from North and *C. g. fregata* from Fregate.

*Cratopus venustus* Galman *et al.* 2012 – Praslin

Galman *et al.* 2012 recognise the *C. segregatus* subspecies as valid: *C. s. segregatus* from Silhouette, *C. segregatus subcinctus* from Praslin and Round

## Nitidulidae

### Cybocephalinae

*Cybocephalus blandus* Endrody-Younga, 1964

*C. compressus* Endrody-Younga, 1964

*C. grouvillei* Endrody-Younga, 1964

*C. mahensis* Endrody-Younga, 1964

*C. minimus* Grouvelle, 1913 = *C. brevis* Grouvelle, 1913

*C. rugatus* Endrody-Younga, 1964

*C. seychellensis* Endrody-Younga, 1964

## Eupraeinae

*Eupraea (Haptoncuria) motschulskyi* Reitter, 1873 – introduced. Kirejtshuk 2005



## **Carpophilinae**

*Carpophilus (C.) delkeskampi* Hisamatsu, 1963 – introduced. Kirejtshuk 2005

## **Meligethinae**

*Pria nitidior* Grouvelle, 1913 = *Microporellus nitidior* (Grouvelle, 1913)

*Pria scotti* Grouvelle, 1913 = *Microporellus scotti* (Grouvelle, 1913)

*Microporellua insulare* Kirejtshuk, 1995 [*M. insularis*] - Praslin

*Microporum popei* Endrody-Younga, 1978 – Aldabra

## **Nitidulinae**

*Phenolia (Lasiodites) picta* (Macleay, 1825) = *Lasiodactylus pictus* (MacLeay, 1825)

*Stelidota explanata* Grouvelle, 1913. Nitidulinae not Meligethinae.

## **Staphylinidae**

*Erichsonius (Sectophilonthus) jelineki* Uhlig & Janak 2009 - Mahé: Trois Frères

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# Animals depicted by Marianne North in her Seychelles paintings

Anthony S. Cheke  
139 Hurst St., Oxford OX4 1HE, UK  
[anthony.cheke@dodobooks.com](mailto:anthony.cheke@dodobooks.com)

**Abstract:** The animals depicted in paintings done by Marianne North in the Seychelles in 1883-4 are identified, and an important 'lost' painting of the extinct Seychelles parakeet *Psittacula wardi* is located and published for the first time.

## Introduction

Marianne North is a celebrated botanical artist who travelled the world in the latter half of the 19<sup>th</sup> century, including in 1883-4, as her penultimate expedition, the Seychelles. There she painted 46 or 47 oils (Nos. 348, 358, 458-501 & possibly 356) that have ever since been on show at the Marianne North Gallery at the Royal Botanic Gardens at Kew, UK (Payne 2011), and at least one other currently in private hands. She is immortalised in Seychelles botany through Joseph Hooker naming the genus *Northea* of the *capucin/kapisen*<sup>1</sup> tree after her (Friedmann 2011), now rare and rated Vulnerable by IUCN. All the paintings discussed below can be found in the online gallery of her paintings (<http://www.kew.org/mng/gallery/africa.html>) under the same numbers; they were also catalogued by anon. (1914), each painting having a fairly detailed description by her botanist friend William Botting Helmsley (Ryall 2009), apparently based on notes by North herself.

Although the botanical subjects of North's paintings were mostly identified by the artist herself, and others have since studied and (mostly) admired them, and her renderings of scenery and architecture are also excellent and atmospheric, her animals have been neglected. Although she often included local wildlife in her compositions showing plants in their natural setting, they are less deft than her plants, but nonetheless identifiable to species. In conjunction with the faunal notes included in her autobiography (North 1892) they provide, in the Seychelles, a useful snapshot of wildlife in a period when there are few other natural history records. Apart from Matyot's (2005) identification of hawk-moths, Ponsonby's (1990) tentative assessment of a single bird, and references to an unpublished image of the extinct parakeet *Psittacula wardi* (e.g. Skerrett *et al.* 2001), it appears that the faunal content of the Seychelles *oeuvre* has not been identified or discussed. The descriptions in anon. (1914) often mention the animals by their common name, as does North (1892) in her autobiography, but that is the limit of the published detail. The discussion here is confined to terrestrial animals, plus a marine turtle.

<sup>1</sup> Originally *Northea seychellana* (Sapotaceae), it is now called *N. hornei* because the seeds were named *Mimusops hornei* before the source tree was recognised by science (Friedmann 1994).

## Identifications

Twelve Seychelles paintings include animals, some acknowledged in the title and/or description, some not. Some of these are also mentioned in the autobiography (North 1892, vol.2), but most are not, though additional species feature there (see below); if there is a mention it is cited. If no specific reference is given, identification and data is from Skerrett *et al.* (2001), Bowler (2006) or Gerlach (2007). For details of the plants, see anon. (1914) and the online gallery, but note that the scientific names of plants in the gallery itself and online have not been updated from the 1914 edition of the catalogue, and a good many have changed since; hence, for dicotyledons, Friedmann (1994) should also be consulted.

In addition to the animals described below, several paintings include chickens and geese, and one (No.479) an unidentified flying creature lower left above a juvenile coco-de-mer palm *Lodoicea maldivica*. No.484 has two tiny unidentified birds and a number of crabs, also too small, on inshore rocks.

### Painting 348: *Fruit de Cythere and Sugar Birds and Nest, Seychelles*

Although this painting is listed and exhibited with those done in South Africa, it is identified with the Seychelles both in its title and the following comments in North's autobiography (1879, 2: 289):

A pair of merles had built their nest close to his house and laid eggs in it, and tiny sun-birds were hard at work at a dangling fragile pouch of cotton from the bombax-trees near, close to the verandah where I worked, hanging it on a drooping leaf-stalk of the *Spondias cytherea*, a tree like a very spreading ash.

This was on Praslin; *Spondias* = 'fruit de Cythère'/'*frisiter* in Indian Ocean French/creole (D'Offay & Lionnet 1982). The sunbirds are not well enough drawn to be positively identified from the painting, and the use of 'sugar-birds' in the title may have misled North herself or her assistants in assigning the image to its place in the gallery. 'Sugar-bird' normally refers to the South African genus *Promerops*, unrelated to sunbirds but also nectar-feeders with long curved bills (e.g. Sinclair *et al.* 1993). The birds depicted are consistent with the only sunbird in the granitic Seychelles, the endemic *Nectarinia dussumieri*; merles, or Seychelles bulbuls, also endemic, are *Hypsipetes crassirostris*.

### Painting 458: *A Swamp Plant and Moorhen, Seychelles*

At first glance this entirely bluish bird would appear to be a *Porphyrio* swamphen, and when I first saw it at Kew my thought was that perhaps the enigmatic *poule bleu* had survived 100 years longer than previously thought (Lionnet 1984, Cheke 2013). That possibility is reinforced by a remark of Mauritius Governor Arthur Gordon (1894, 1: 220), on a visit in 1871, that on Praslin "waterfowl flitted about, among them the exquisite *Poule bleue* of the West Indies<sup>2</sup>". However although the body plumage of the bird illustrated is wrong, and it lacks the trademark white line on the flank, the beak and leg colours are correct for *Gallinula chloropus*, the common moorhen that is

<sup>2</sup> American purple gallinule *Porphyrio martinica*.

widespread on Indian Ocean islands including the granitic Seychelles. Rather than the original *poule bleue* surviving, it is possible that both visitors happened to see vagrant Allen's gallinules *Porphyryula alleni* (see Skerrett *et al.* 2001), perhaps less infrequent then, and that North confused them with Moorhens also present, and hence produced the chimaera in the painting. The description (anon. 1914) adds, irrelevantly, "the Moorhen is remarkable for its very large feet".

Painting 459: *Wormia and Flagellaria in the Seychelles*

The hawk-moth illustrated is *Hippotion osiris* (Matyot 2005), a species found in the Seychelles and Madagascar.

Painting 469: *Veloutier Blanc and pair of Martins, Seychelles*

'Martin'/*marten* is the local French/creole name for the common myna *Acridotheres tristis* (d'Offay & Lionnet 1982, Skerrett *et al.* 2003), an Indian species introduced into the Seychelles from Mauritius around 1830-35 (Cheke 2010). North (1879, 2: 290), on Praslin, described the birds she illustrated; mynas are good mimics:

There were also two martins, much like the mynah-birds of India, with yellow beaks and feet. They were most impudent, and would come and perch on the chairs of the verandah, chase the cocks and hens, and defy the dogs, whistling most pertinaciously, and calling "Toby, Toby, Toby !" till the dog ran half mad.

Painting 472: *Saponaire or Periwinkle and Green Frogs in Mahe*

The frogs depicted are *Tachycnemis seychellensis*, an endemic species widespread on the larger islands (Gerlach 2007). At the foot of the picture there is a black snail which most closely resembles the black form of the endemic species *Pachnodus kantilali*, found only on the hills of Mahé above 600m a.s.l. (Gerlach 1987, Justin Gerlach pers.comm.); the artist may have found it when she climbed up over the central ridge to Venn's Town (2: 304-5).

Painting 477: *Female Coco de Mer bearing Fruit covered with small Green Lizards*

Painting the palm fruits on Curieuse, North picked up the characteristic behaviour of day geckos crowding onto *Lodoicea* infructescences. They are too tiny to be identified directly from the painting, but as she called them 'small' they will have been *Phelsuma astriata*, which fits their size as against the fruit in the artwork. She commented (North 1879, 2: 291):

I rested my painting-board on one of the great fan leaves, and drew the whole mass of fruit and buds in perfect security, though the slightest slip or cramp would have put an end both to the sketch and to me. Bright green lizards were darting about all the time, over both the subject and the sketch, making the nuts and leaves look dull by contrast.

Painting 482: *Two trailing-plants with Lizard and Moth from Ile Aride, Seychelles*

The hawk-moth is *Hippotion eson* (Matyot 2005), the day-gecko *Phelsuma*

*astriata*, the only species present on Aride (Cheke 1984, Radtkey 1996).

Painting 483: *Emile's Palm House, Praslin, Seychelles*

On the beach in front of the house is a very large hawksbill turtle *Eretmochelys imbricata*, locally known as *caret/kare* (d'Offay & Lionnet 1982), the source of commercial tortoise-shell. Of a different occasion off La Digue she wrote (1879, 2: 295):

...once they speared a hawk's-head turtle or "carre" which a shark was trying to get into his mouth : a rather large morsel, as it was over three feet long. I bought it of the sailors for £2 : 10s., the value of the tortoise-shell back. Catching them is the principal aim of sailors in those islands, and they divide the profits made by each boat, one man often making ten pounds in a season. The one I bought was found to be full of eggs, which were collected in a pail, buried in the sand near the house, and kept till they hatched, after which they were kept another six weeks with difficulty, as they have an inclination to run into the sea as soon as they leave their shells, and would be quickly gobbled up if they did. They are fed on fish, and some of the natives keep them till their shells become saleable ; but to do this is more trouble than they are worth.

The description (anon. 1914) adds: "secured to one of the trees is a Hawkshead Tortoise, whose shell is the fortune of the fishermen of the islands".

Painting 487: *Flowers of a bush and Pitcher Plant, Mahe*

This picture includes two chameleons *Archaius* (formerly *Calumma*) *tigris*, an endemic species found only on Mahé, Silhouette and Praslin (Gerlach 2007).

Painting 489: *A Native Orchid and Butterflies, Mahe, Seychelles*

The two butterflies are Seychelles crow *Euploea mitra*, now Endangered (Gerlach *et al.* 2005) and apparently confined to the central ridge on Mahé (Bowler 2006).

Painting 496: *The Seychelles Pitcher Plant in blossom and Chameleon*

Another representation of *Archaius tigris*.

Painting 501: *Foliage, Flowers, and Fruit of the Capucin Tree of the Seychelles*

Unmentioned in either title or description is the bright red male cardinal fody *Foudia madagascariensis*; Ponsonby (1990) tentatively identified the bird, and rightly pointed out that it should have had a black bill<sup>3</sup>. The species was introduced on Mahé around 1860, and North's mention of cardinal fodies on Praslin is the first for that island following their introduction to the granitics (Cheke & Rocamora in press), and she also reported paradise flycatchers *Terpsiphone corvina* there, which have since died out:

<sup>3</sup> Adult male *Foudia madagascariensis* have black bills in full red nuptial plumage (as painted by North), but in eclipse plumage have palish brown bills like females (Skerrett *et al.* 2001).

We walked across the island to the north shore, the last part of the road being through miles of cocoa-nut plantations, where we saw some few birds, including “whydah-birds” with long tails [i.e. flycatchers<sup>4</sup>], also a red foudia with its brown wives. The Creoles had driven nearly all birds away, and they had taken refuge on an outside island called Marianne, from whence the doctor had lately imported some of different sorts to Praslin, much to the disgust of the natives.

This seems to imply that ‘the doctor’ (James Brooks, see below) had already been supplementing flycatcher numbers on Praslin from Marianne, then presumably still rat-free with its original forest (Cheke 2013), and may have been responsible for introducing the cardinal fody to Praslin, which would explain why the ‘natives’ were disgusted. It is a major pest of rice crops, and was generally considered by the end of the 19th century to be the reason why rice cultivation had been abandoned in the islands (Cheke & Rocamora in press).

Private collection: [*Caesalpinia* and two parakeets, Mahé; Fig 1.]

This painting and its subjects are described in North’s autobiography (1879, 2: 302) in the following terms:

He [‘Dr B.’<sup>5</sup>] and his Greek wife were very kind and hospitable in their offers to me. I went one day to their house, and painted their parrots, which came originally from Silhouette: queer, misshapen birds, with enormous beaks and patches of red and yellow badly put on, one of them having a black ring round its neck. Both were quite helplessly bullied by common pigeons, which came and ate up their food, while they jabbered in a melancholy way, and submitted. They had absolutely no tops to their heads, which perhaps accounted for their stupidity. They had a stand on the back verandah, where they slept and were fed. They were not tied up, but went and stole their own fruit off the neighbouring trees.

The birds are endemic Seychelles parakeets *Psittacula wardi*, which became extinct around 1900 (Skerrett *et al.* 2001, Cheke 2013). This is the only time the species was depicted alive, and the left-hand bird, showing paler underparts and lacking a neck ring, is clearly a juvenile, whose plumage was previously unknown. Although, as mentioned earlier, North’s painting was known from her writings, no representation of it has previously been published; her own title for this image is not known. The painting itself is currently owned by the family of Tom North, great grandson of Marianne’s brother Charles. It was bought back by the family at auction from Bonhams in the early 1990s (Tom North pers. comm.); precise sale details are not available, nor the

<sup>4</sup> The local name of the paradise flycatcher is *veuve/vev* (Skerrett *et al.* 2003), ‘widow’, which North, having recently been in South Africa, assimilated to the unrelated but similarly long-tailed, largely black, widow-birds *Euplectes* spp. and whydahs *Vidua* spp. (Sinclair *et al.* 1993).

<sup>5</sup> Personal names were all included in full in North’s original manuscript, still in the family archives, but edited out by her sister when preparing it for publication (Tom North, pers. comm.). ‘Dr B.’ is however easily identifiable from island histories as colonial medical officer Dr James Brooks (see McAteer 2000), but in any case the words “Dr and Mrs Brooks” have escaped the editor a few lines further on!





**Fig.1.** Marianne North's painting of the extinct endemic Seychelles parakeet *Psittacula wardi*, with the tropical garden ornamental *Caesalpinia pulcherrima*, originally from tropical America (photo by Bob Billington, reproduced with permission of Tom North).



intervening whereabouts of the painting. The colours in the parrot painting are a lot more muted than North's other oils done in the Seychelles, both before and after this one; it is possible that the different conditions it has experienced compared with the Kew collection has resulted in some fading.

One might expect 'common pigeons' to have been feral pigeons *Columba livia*, but these appear not to have been introduced until the 1970s (Skerrett *et al.* 2001), and given the remarks North made about very bold 'wild doves' (below), it seems probable that the bullies were in fact Malagasy turtle doves *Nesoenas picturata*.

### Animal observations not echoed in paintings

North's autobiography (1897, vol.2) includes further animal notes, which warrant some comment. Almost the first things she noticed on arrival at Mahé were "exquisite turquoise crabs with red legs", semi-terrestrial fiddler crabs *Uca* sp., probably *U. tetragonon*<sup>6</sup>. Later, on Curieuse, she mentioned big black crabs and 'soldier-crabs' (i.e. terrestrial hermit crabs), but not in enough detail to identify. On Praslin (p.296-7) she discussed Dr Hoad's former pet flying fox *Pteropus seychellensis*, and on Mahé *chez* 'Mrs E.'<sup>7</sup> (p.300) "Four wild doves also used to come and feed on the verandah, so impudent that they never moved away when the dog Snap walked through them". These were no doubt the Malagasy turtle dove *Nesoenas picturata*, probably the nominate form *N. p. picturata*, which had more or less replaced the native race *rostrata* on Mahé a decade earlier (Oustalet 1878). On Long Island, not long before her departure, she watched a Seychelles kestrel *Falco araea* catch a day-gecko *Phelsuma* sp.:

One afternoon I heard a rustle close to where I was sitting under the trees, and saw a small hawk, no bigger than a thrush, pick up a green lizard, look defiantly at me for a moment, then fly away with its body. The tail fell to the ground, and began waltzing round and round. I took out my watch and timed how long it continued to move; it was quite half an hour, the last movement being just at the tip of the tail, and by that time it was quite covered with small black ants, which carried it off bit by bit, not only into their principal hole, but into little back doors which they had in a long crack of the dry ground. The next morning there was none of the tail to be found.

This is the first direct observation of the kestrel feeding, although Newton (1867) had noted unspecified lizards in the gut of specimens he collected.

<sup>6</sup> Bowler (2006; poor photo) only takes fiddler crabs to genus, High (n.d.) has a better photo but also only mentions the genus – there are 3 species in the Seychelles (Haig 1984), and identification to species is from photos online at: [http://www.fiddlercrab.info/uca\\_photos.html](http://www.fiddlercrab.info/uca_photos.html). Ponsonby's biography (1990) mentions in the same sentence as the fiddler crabs that North saw "spiders who [sic] were 'rampant and enormous'" – there seems to be no such reference in the entire text of volume 2 of North's autobiography (1879). I searched the online OCR 'full text' on Archive.org (the Toronto library version, not the very poorly OCR'd Google Books version), so perhaps this information came from an unpublished letter; there are, of course, abundant, large and conspicuous orb-web spiders *Nephila inaurata* in the Seychelles (Bowler 2006).

<sup>7</sup> Presumably the wife of Henry Estridge, Collector of Taxes (McAteer 2000); North described his office as "the Treasury".

She mentions seabirds only twice (pp.293-4, 305). From high up on Mahé “one saw a long stretch of wild mountain coast, and many islands, some 2000 feet below, across which long-tailed boatswain-birds were always flying”, as these birds, white-tailed tropic-birds *Phaethon lepturus*, still do. For the other species, on Curieuse, she, or her editor, was fed a seriously wrong scientific name:

There was no water, only that which filtered through the sand into wells from the sea, and the low bushes near the rocks were covered with small terns (*Sterna velox*) with white heads, so tame that they let one take them off their nests without attempting to escape. Cruel little Johnnie collected some dozen, and tied them in a bunch by their feet, dying and dead, to send to his mother by the next boat. The owner of the island was making quite a fortune by selling them in Mahe to make pigeon-pies (very fishy).

Tame white-headed terns must have been Fairy Terns *Gygis alba*, for which culinary use is generally unusual. ‘*Sterna velox*’ was a combination used at the time for crested terns *Sterna* (= *Thalasseus*) *bergii*.

“Centipedes”, wrote North (2: 301) “are the only evil things in the island” (Mahé), referring to animals 3-5 inches long (75-125mm) with a sting like “like touching a red-hot poker”, presumably *Scolopendra subspinipes*, which can reach 8”/200mm (Bowler 2006).

Finally North discussed the keeping of giant tortoises *Dipsochelys dussumieri* (*Aldabrachelys gigantea* auct.) (pp.287-8, 296-7); her brief but important contribution is discussed by Cheke & Bour (2013).

## Images of Madagascar wildlife

Displayed with paintings done in South Africa, and included with that country in the printed catalogue are two paintings of subjects from Madagascar that also include animals. However, one of these, and possibly both, were painted in the Seychelles. Although North intended to visit Madagascar (& Mauritius) after South Africa, she had to abort the trip from ill-health and never went there (North 1879, anon. 1914).

### Painting 356: *Angraecum* and *Urania* Moth of Madagascar

Both orchid (*A. sesquipedale*) and moth are Malagasy endemics, painted according to Payne (2011) in South Africa. The moth an excellent rendering of what is now called the Madagascar sunset moth *Chrysidia rhipheus*<sup>8</sup>. There is nothing in the autobiography to indicate where this might have been painted, but climatically the Seychelles would have been a more likely place to cultivate the orchid. The moth’s caterpillar has very specific food requirements, eating only *Omphalea* spp. (Euphorbiaceae), of which no species occur in either South Africa or the Seychelles. Hence it appears that North must have painted *Chrysidia* from a preserved specimen. There are two native species of *Angraecum* in the Seychelles (Lionnet n.d., Jolliffe

<sup>8</sup> Identification and life-history information from the excellent article in Wikipedia, accessed 31.7.2013 ([https://en.wikipedia.org/wiki/Chrysidia\\_rhipheus](https://en.wikipedia.org/wiki/Chrysidia_rhipheus)).

2010), both clearly different from the Malagasy species depicted in No.356; North painted the commoner one *A. eburneum*, *fler payanke* [*fleur paille-en-queue*] now the Seychelles national flower, in No.489.

#### Painting 358: *Ordeal Plant or Tanghin and Parakeets of Madagascar*

The only references to seeing the ‘ordeal plant’ or ‘tanghinia’ in the autobiography are in the Seychelles (1879, 2: 300 & 304), and it is presumably there that she painted it. The plant in the painting appears not to be the small-flowered *Cerbera venenifera*<sup>9</sup>, typical of Madagascar, but the somewhat larger flowered *C. manghas* still common in the Seychelles; the two forms may be conspecific (Friedmann 1994). At the time the accompanying grey-headed lovebirds *Agapornis canus*, Malagasy endemics, were popular cage-birds in the colonial islands of the Indian Ocean, establishing feral populations on several (e.g. Cheke & Hume 2008), and are very likely to have been kept in the Seychelles as they were elsewhere – although they did not escape into the wild there until some 20 years later (Skerrett *et al.* 2001).

#### Acknowledgements

My thanks go to Michelle Payne at Kew for forwarding my initial query about the parrot painting to Marianne’s North’s great great-nephew Tom North, to him for kindly arranging for the painting to be photographed and for permission to reproduce it, and to Bob Billington for the photo itself. Deborah Cliffe of Bonhams auctioneers kindly tried, but failed, to trace the sale record of the parrot painting. Justin Gerlach helpfully identified the endemic snail in painting 472, and alerted me to a recent generic change in the endemic chameleon.

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<sup>9</sup> The species is given as *C. tanghin* in the catalogue (anon. 1914). The Malagasy and Seychelles forms had not been distinguished at the time of North’s visit (Baker 1877), but both apparently occurred together in the Seychelles in the 19<sup>th</sup> century (Friedmann 1994). The surviving Seychelles plant is still called *tanghin* in local French/creole (*ibid.*).

*Phelsuma* 21: 4-19.

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## The Lepidoptera of Curieuse Island, Seychelles

Patrick J. Woods  
Global Vision International (GVI),  
Curieuse Island, SEYCHELLES  
[p\_j\_woods@hotmail.co.uk]

### Introduction

Curieuse Island is the fifth largest inner granitic Seychelles Island, and has an area of 286ha (Hill *et al.* 2002). Curieuse is a government owned National Park and is managed by the Seychelles National Parks Authority (SNPA), a parastatal organisation. Curieuse has several associated habitats; the bulk of the island consists of central hills with exposed red granite, up to 172m (Hill *et al.* 2002). Surrounding these hills are forested lowland coastal plateau areas. There are four main plateau areas, Anse Badamier on the north of the island and Anse Jose to the south, while Baie Laraie has two distinct plateau areas, the area of mangroves in the north west of the bay and surrounding the Park Rangers' Headquarters to the east of the bay (Hill *et al.* 2002) (Figure 1).

Lepidoptera in the inner granitic Seychelles Islands have been well studied on some individual islands (Lawrence 2005) and as described in the Indian Ocean Biodiversity Assessment 2000-2005 (Gerlach 2003). However, there is little comprehensive information available on the Lepidoptera that can be found on Curieuse Island. An overview of all the taxa found on Curieuse by Hill *et al.* 2002 described 2 species of butterfly (*Zizeeria knysa* and *Leptotes pirithous*) as present on Curieuse. However, no information was provided on the moth species found on Curieuse. Gerlach and Matyot (2006) collected and collated records for the Indian Ocean Biodiversity Assessment 2000-2005 (Gerlach 2003). Eleven species of lepidoptera were described as present on Curieuse in the monograph (Gerlach & Matyot 2006) that followed the Indian Ocean Biodiversity Assessment 2000-2005 (Gerlach 2003). A permanent scientific expedition base on Anse Jose on Curieuse Island is currently occupied by Global Vision International (GVI), facilitating the long term, regular use of light traps to investigate the species of macro-lepidoptera on Curieuse. The aim of this study was to produce a species list of the lepidoptera found on Curieuse Island.

### Methods

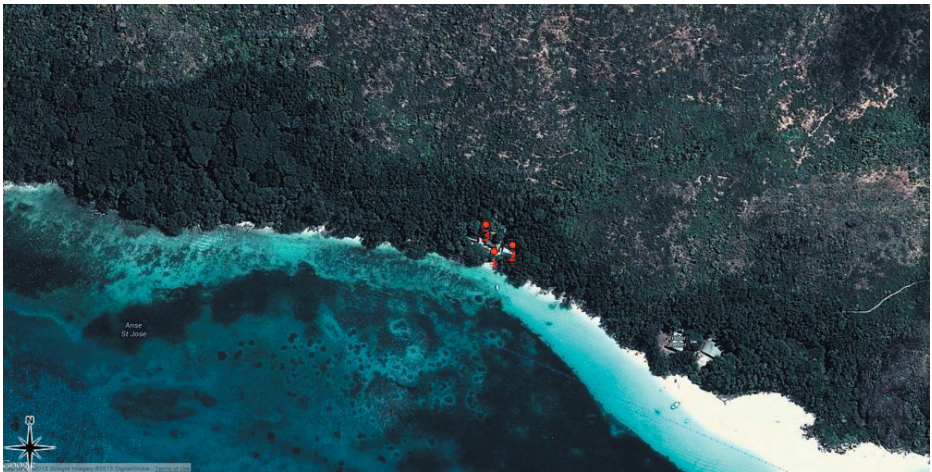
This study took place between 9<sup>th</sup> April 2013 and 13<sup>th</sup> September 2013 at the site of a former leper colony, occupied by GVI on the coastal plateau at Anse Jose on the south coast of Curieuse Island. Samples were collected from 3 sites on the coastal plateau at Anse Jose (Fig. 2). Site 1 was situated in a small man-made clearing, surrounded by mature coastal trees, such as *Calophyllum inophyllum* (takamaka). Sites 2 and 3 were situated under the canopy of mature coastal forest, which included both palm and tree species. A Skinner trap with a 15w actinic bulb powered by a 12v battery was used



to attract specimens. Specimens were collected at least once a week throughout the study period, unless poor weather prevented the use of the light trap. Any opportunistic sightings of species around lights from occupied buildings of the expedition base were also recorded. The monograph 'Lepidoptera of the Seychelles Islands' (Gerlach & Matyot 2006) was used to identify specimens. Lepidoptera taxonomy is as described in Gerlach & Matyot (2006) and IUCN Red List Category Assessments from Gerlach *et al.* (2005) and Gerlach & Matyot (2006) are used.



**Figure 1.** A satellite image of Curieuse Island, the main beaches and landmarks are labelled. The red dots indicate the site of the expedition base currently occupied by GVI and the 3 sites sampled for Lepidoptera.



**Figure 2.** A satellite image of Anse Jose, on the south coast of Curieuse Island. The red dots indicate the 3 sites sampled for Lepidoptera at the GVI expedition base.

## Results

During this study a total of 30 species of Lepidoptera were recorded on Curieuse Island over a 5 month period. The species recorded are listed in Table 1. An additional 10 species were recorded on Curieuse in 2001 and 2002 (Table 2) during data collection for the Indian Ocean Biodiversity Assessment 2000-2005, summarised in the monograph by Gerlach and Matyot (2006). Only one species, *Dirades theclata* was recorded by Gerlach and Matyot (2006) and also observed during the current study on Curieuse. The total number of species of lepidoptera recorded on Curieuse was 40. Of these 40 species 17 (42.5%) were species endemic to The Seychelles, 9 species (22.5%) are found in the tropics, 6 species (15%) have wide distributions across Africa, Asia and Europe, 5 species (12.5%) are only found in Africa and 3 species (7.5%) were restricted to the Indo-Pacific.

All species, apart from one, *Lamoria anella* (Fig. 3), are listed as Least Concern under the IUCN Red List Criteria (Gerlach *et al.* 2005). *Lamoria anella* is listed as Data Deficient. *Lamoria anella* was encountered on 7 occasions and a total of 18 individuals were observed during this study between 09/04/2013 and 15/06/2013. Only *Dirades theclata* and *Dudua aprobola* were encountered more times 58 and 62 times respectively. *Dirades theclata* and *Dudua aprobola* were both observed at 11 different times throughout each month of data collection for the study. In addition, 2 species of butterfly *Zizeeria knysa* and *Lampides boeticus* were regularly observed during the day throughout the study period, with *Zizeeria knysa* observed daily. The migratory *Hypolimnas misippus* was observed on 3 occasions during April 2013. Of the 30 species recorded in this study, 11 species were only observed once during the study period.

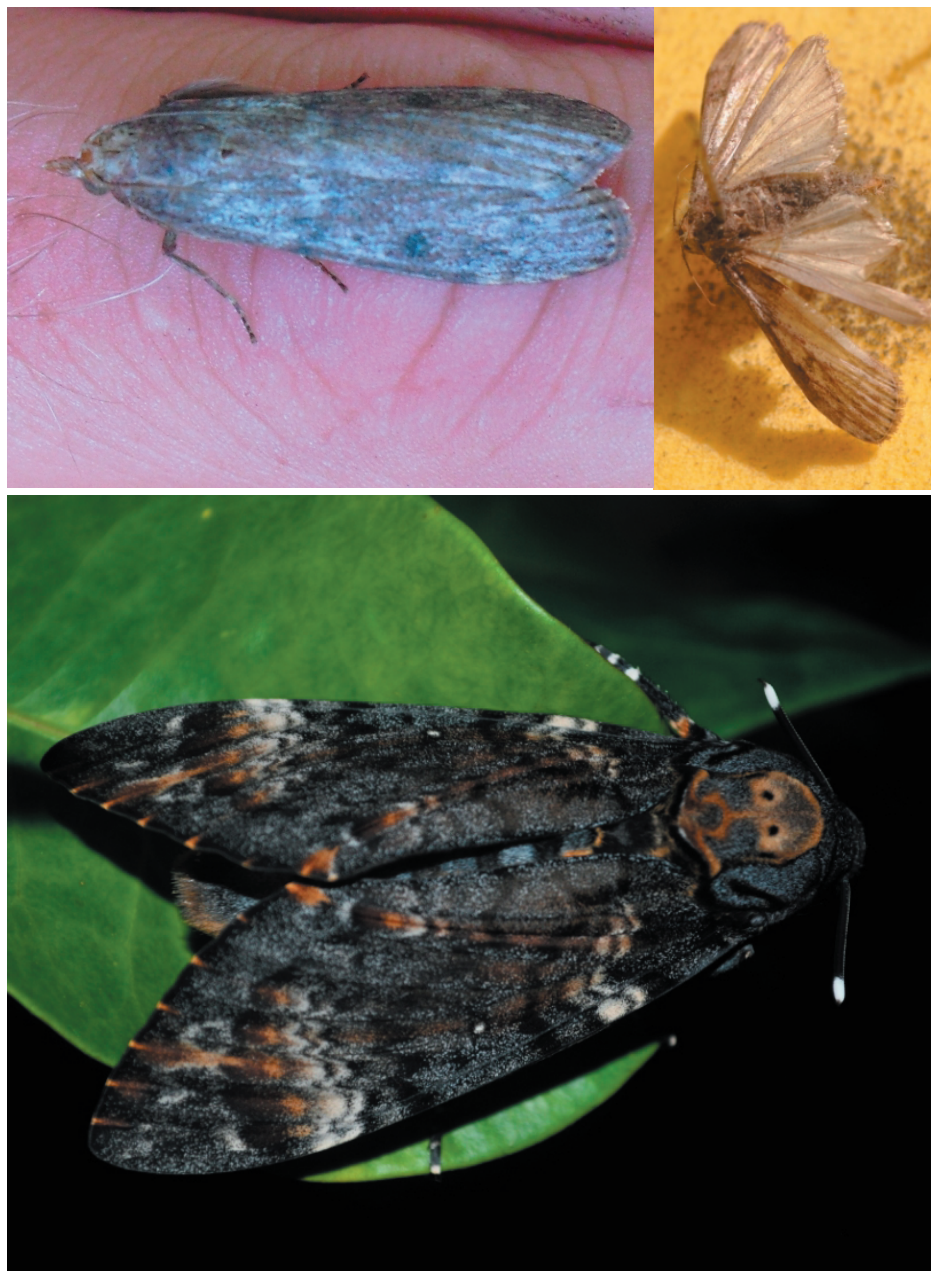
## Discussion

The species list presented here is the most comprehensive and systematic study to date of the Lepidoptera that occur on Curieuse Island and has made a significant start to documenting the Lepidoptera of Curieuse. Curieuse appears to be relatively species poor in Lepidoptera when compared to other inner granitic islands, supporting only 40 species. Mahe supports 345 species and Silhouette supports 288 species (Gerlach & Matyot 2006). However, Praslin only supports 42 species (Gerlach & Matyot 2006). Curieuse is approximately 1km from Praslin, is geologically similar and has a similar climate to Praslin (Hill *et al.* 2002). Therefore, a comparison between Praslin and Curieuse is likely to be more useful than a comparison with Mahe or Silhouette.

In total, 552 species of lepidoptera have been recorded in the Seychelles Islands, 275 (50%) of which are endemic to the Seychelles (Gerlach & Matyot 2006). This pattern is similar to the pattern observed in this study on Curieuse, where 42.5% of the species recorded were endemic species. Although Curieuse Island only supports 40 species of Lepidoptera, a high proportion of these are endemic to the Seychelles islands. Curieuse Island also supports a high proportion of endemic flora (Hill *et al.* 2002) which may explain the high proportion of endemic species of lepidoptera. However, further research would be needed to confirm this hypothesis.

This study is unlikely to have been able to produce a complete species list of Lepidoptera supported by Curieuse Island. New species were recorded throughout the





**Figure 3.** Lepidoptera recorded on Curieuse Island.  
 a & b) *Lamoria anella*, c) *Acherontia atropos*.  
 Photos: a & c - K. Quinton, b - P. Woods.

study period and the study period did not cover a full year. Therefore, species with flight times outside of the period studied here will have been overlooked. This study was confined to one area of the coastal plateau at Anse Jose and no observations were made in additional habitats, for example mangroves, or elevated areas. However, the habitat on the coastal plateau of Anse Jose was described as ‘exceptionally rich’ in the Indian Ocean Biodiversity Assessment (Gerlach 2003) and so may support a greater species richness of Lepidoptera than other areas of Curieuse. However, study into further areas of Curieuse would be needed to confirm this. A greater range in island elevation rather than a larger island area leads to a greater species richness of Lepidoptera (Gerlach & Matyot 2006). Further study into additional habitats and particularly different elevations throughout an entire year could reveal the presence of further species on Curieuse Island.

### **Acknowledgements**

My thanks go to Dr. Justin Gerlach and Mr. Pat Matyot for help with identification of specimens. My thanks also go to Seychelles National Parks Authority (SNPA) and Global Vision International (GVI) for their collaboration which made this study possible.

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## Appendix

**Table 1.** The species of Lepidoptera recorded on Curieuse Island, along with their global distribution (Gerlach & Matyot 2006) and IUCN Red List Category (Gerlach *et al.* 2005). LC is Least Concern and DD is Data Deficient. The total number of individuals of each species seen throughout the study period is also included.

Species	Distribution	IUCN Category	Number of individuals seen
<i>Tiquadra gypsatma</i> (Meyrick, 1911)	Endemic	LC	5
<i>Ethmia nigroapicella</i> (Saalmüller, 1880)	Indo-Pacific	LC	16
<i>Stathmopoda d.daubanella</i> (Legrand, 1958)	Endemic	LC	1
<i>Stathmopoda epilampra</i> (Meyrick, 1911)	Endemic	LC	4
<i>Mesophleps safranella</i> (Legrand, 1965)	Endemic	LC	4
<i>Autocharis amethystina</i> (Swinhoe, 1894)	Palaeotropical	LC	2
<i>Cirrhochrista perbrunnealis</i> (Fletcher, 1910)	Endemic	LC	1
<i>Omiodes indicata</i> (Fabricius, 1775)	Pantropical	LC	4
<i>Lamoria anella</i> (Schifferrmüller, 1775)	Cosmopolitan	DD	18
<i>Etiella zinckenella</i> (Treitschke, 1832)	Pantropical	LC	3
<i>Phycita gloriosella</i> (Legrand, 1965)	Endemic	LC	3
<i>Endotricha mesenterialis mahensis</i> (Whalley, 1963)	Endemic	LC	1
<i>Hypsopygia mauritialis</i> (Boisduval, 1833)	Asia and Madagascar	LC	1
<i>Dudua aprobola</i> (Meyrick, 1886)	Indo-Pacific	LC	62
<i>Eccopsis incultana</i> (Walker, 1863)	Africa	LC	1
<i>Polydesma umbricola</i> (Boisduval, 1833)	Palaeotropical	LC	1
<i>Chloroclystis nigella</i> (Joannis, 1906)	Africa	LC	1
<i>Petrodava madecassaria</i> (Boisduval, 1833)	Africa	LC	1
<i>Thalassodes quadraria</i> (Guenée, 1875)	Palaeotropical	LC	6
<i>Dirades theclata</i> (Legrand, 1966)	Palaeotropical	LC	58
<i>Euproctis pectinata</i> (Fryer, 1912)	Endemic	LC	3
<i>Achaea catella</i> (Guenée, 1852)	Africa	LC	1
<i>Remigia frugalis</i> (Fabricius, 1775)	Palaeotropical	LC	1
<i>Stictoptera poecilosoma</i> (Saalmüller, 1880)	Indian Ocean	LC	4
<i>Acherontia atropos</i> (Linnaeus, 1758)	Africa and Europe	LC	2
<i>Lampides boeticus</i> (Linnaeus, 1767)	Europe, Palaeotropical	LC	4
<i>Lepotes p. pirithous</i> (Linnaeus, 1767)	Europe and Africa	LC	1
<i>Zizeeria knysa</i> (Trimen, 1862)	Africa, Europe, Asia	LC	5
<i>Hypolimnas misippus</i> (Linnaeus, 1764)	Palaeotropical	LC	3
<i>Melantis leda</i> (Linnaeus, 1758)	Palaeotropical	LC	2

**Table 2.** Additional species recorded as present on Curieuse by Gerlach & Matyot 2006, along with their global distribution and IUCN Red List Category (Gerlach *et al.* 2005) (LC = Least Concern).

Species	Distribution	IUCN Red List Category
<i>Pitharca chalinaea</i> (Meyrick, 1908)	Africa	LC
<i>Amphixystis sicaria</i> (Meyrick, 1911)	Endemic	LC
<i>Caloptilia megalaurata</i> (Legrand, 1966)	Endemic	LC
<i>Ascalenia pseudofusella</i> (Legrand, 1965)	Endemic	LC
<i>Labdia tentoria</i> (Meyrick, 1911)	Endemic	LC
<i>Pyroderces firma</i> (Meyrick, 1911)	Endemic	LC
<i>Pyroderces jonesella</i> (Legrand, 1965)	Endemic	LC
<i>Pyroderces longalitella</i> (Legrand, 1965)	Endemic	LC
<i>Metachanda brunnepunctella</i> (Legrand, 1965)	Endemic	LC
<i>Metachanda fortunata</i> (Meyrick, 1911)	Endemic	LC

## New records of Hymenoptera from Bird (Republic of Seychelles)

Michael Madl

2. Zoologische Abteilung, Naturhistorisches Museum,  
Burgring 7, 1010 Wien, Austria.  
*michael.madl@nhm-wien.ac.at*

### Introduction

Recently I received from my colleague Manfred A. Jäch (curator of Coleoptera) several specimens of Hymenoptera from Bird for identification, which have been found in a box with Seychellois Coleoptera. The material contains only two species of the family Vespidae (*Delta alluaudi* (Perez, 1895), *Polistes olivaceus* (DeGeer, 1773) and one species of the family Apidae (*Xylocopa caffra* (a Linné, 1767)). *Delta alluaudi* is a first record for the fauna of Bird. The Hymenoptera of the Republic of Seychelles have been reviewed by several authors in Gerlach (2013: 230 – 342).

The small and flat coralline islands Bird (1 km<sup>2</sup>) and Denis (1,4 km<sup>2</sup>) are situated at the northern edge of the Seychelles Bank lying about 90 or 80 km North of Mahé respectively. The distance between both islands is more than 50 km. The most important papers on the fauna and flora have been published by Feare (1979), Stoddart & Fosberg (1981) and Hill *et al.* (2002a, b). The latter ones include also species lists of Hymenoptera. Both islands have a depauperate Hymenoptera fauna in relation to the larger granitic islands characterized by non endemic species. Till now 20 species have been recorded from Bird and 10 species from Denis (see table 1).

The material is deposited in the Natural History Museum in Vienna (Austria). I would like to thank Manfred A. Jäch (Natural History Museum Vienna, Austria) for making available the material for study and Manulea Vizek (Natural History Museum Vienna, Austria) for her help in many ways.

### Symbols used:

§ male

\$ female

### Faunistics

Family Vespidae

Subfamily Eumeninae

*Delta alluaudi* (Pérez, 1895)

Material examined: Bird: 3 \$\$ November 1981 leg. H. Kraus.

This first record is a surprise, because *Delta alluaudi* is not mentioned in Hill *et al.* (2002a). It was collected on Denis about 75 years ago (Meade-Waldo 1912: 43). *Delta*

*alluaudi*, an endemic species of the Inner Seychelles, is also known from following islands: Mahé, Round (off Mahé), Silhouette, North, Praslin, Cousin, Marianne, Aride and Denis.

#### Subfamily Polistinae

*Polistes olivaceus* (DeGeer, 1773)

*Polistes olivaceus* (DeGeer, 1773): Vesey-Fitzgerald 1957: 362 (Bird), Hill *et al.* 2002a: 19 (Bird).

Material examined: Bird: 3 \$ November 1981 leg. H. Kraus.

*Polistes olivaceus* is widely in the southern Palaearctic, Ethiopian, Oriental and Australian Region. In the Malagasy Subregion it is known from Madagascar, Réunion, Mauritius and Rodrigues. In the Republic of Seychelles *Polistes olivaceus* is also recorded from several islands of the Inner Seychelles (Mahé, Cachée, Conception, Moyenne, Thérèse, Silhouette, North, Praslin, Aride, Curieuse, La Digue, Félicité, Grande Soeur, Marianne, Denis) and Amirantes (D'Arros, Desroches).

#### Family Apidae

##### Subfamily Xylocopinae

*Xylocopa caffra* (a Linné, 1767)

*Xylocopa caffra* (a Linné, 1767): Hill *et al.* 2002a: 18 (Bird), 19 (biology, as *Xylocopa* sp.).

Material examined: Bird: 3 §§ November 1981 leg. H. Kraus.

*Xylocopa caffra* is widely distributed in the Ethiopian Region and in the Malagasy Subregion it is known from Comoros (Grande Comore, Moheli, Anjouan) and Mayotte. In the Inner Seychelles *Xylocopa caffra* is also recorded from Mahé, Chauve Souris (off Mahé), Conception, Thérèse, Silhouette, North, Praslin, Cousin, Cousine, Curieuse, Félicité, Grande Sœur, Marianne, Aride and Denis. Notes on the biology have been published by Guerrieri *et al.* 2013 and Hölzler & Madl 2013.

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**Table 1:** List of Hymenoptera recorded from Bird and Denis.

Family	Subfamily	Species	Bird	Denis
Chalcididae	Chalcidinae	<i>Brachymeria lepida</i> (Masi, 1917)		X
Formicidae	Dolichoderinae	<i>Tapinonoma m. melanocephalum</i> (Fabricius, 1793)	X	
		<i>Technomyrmex albipes</i> (Smith, 1861)	X	X
	Formicinae	<i>Anoplolepis gracilipes</i> (Smith, 1857)	X	X
		<i>Brachymyrmex cordemoyi</i> Forel, 1895	X	
	Myrmicinae	<i>Cardiocondyla emeryi</i> Forel, 1881	X	X
		<i>Pheidole megacephala</i> (Fabricius, 1793)	X	
		<i>Pheidole parva</i> Mayr, 1865	X	
		<i>Pheidole punctulata</i> (Mayr, 1866)	X	
		<i>Solenopsis seychellensis</i> Forel, 1909	X	
		<i>Strumigenys emmae</i> (Emery, 1890)	X	
		<i>Tetramorium bicarinatum</i> (Nylander, 1846)	X	
		<i>Tetramorium lanuginosum</i> Mayr, 1870	X	
		<i>Tetramorium simillimum</i> (Smith, 1851)	X	
	Ponerinae	<i>Leptogenys maxillosa</i> (Smith, 1858)	X	X
		<i>Odontomachus simillimus</i> Smith, 1858	X	
Scoliidae	Campsomeriinae	<i>Afroscolia ruficornis</i> (Fabricius, 1793)	X	
Vespidae	Eumeninae	<i>Delta alluaudi</i> (Pérez, 1895)	X	X
	Polistinae	<i>Polistes olivaceus</i> (DeGeer, 1773)	X	X
Apidae	Xylocopinae	<i>Ceratina madecassa</i> Friese, 1900		X
		<i>Xylocopa caffra</i> (a Linné, 1767)	X	X
Halictidae	Halictinae	<i>Lasioglossum mahense</i> (Cameron, 1907)		X
Megachilidae	Megachilinae	<i>Megachile seychellensis</i> Cameron, 1907	X	



























































































































































































